Universidade de Aveiro Departamento de Biologia
Ano 2015

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The effects of Wildfire on Lotic Macroinvertebrate Communities in Portugal

Os Efeitos dos Fogos Florestais nas Comunidades de Macroinvertebrados Lóticos em Portugal

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Tese apresentada à Universidade de Aveiro para cumprimento dos requisitos necessários à obtenção do grau de Doutor em Biologia, realizada sob a orientação científica do Doutor Kieran Andrew Monaghan,Investigador Auxiliar do Departamento de Biologia da Universidade de Aveiro e do Professor Doutor Amadeu Mortágua Velho da Maia Soares, professor catedrático do Departamento de Biologia da Universidade de Aveiro.

Apoio financeiro da FCT e do FSE no âmbito do III Quadro Comunitário de Apoio.

Referência da bolsa:
SFRH/BD/43936/2008

“Quer o Anjo da Guarda dizer com as suas palavras,

que muito mais difícil que responder, é perguntar.”

Almada Negreiros

o júri

presidente

Prof. Doutor Domingos Moreira Cardoso
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vogais

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agradecimentos

Agradeço ao meu orientador, Doutor Kieran Monaghan ter partilhado comigo o seu entusiasmo pela Ecologia e por sempre ter estimulado a minha independência e sentido crítico.

Agradeço ao Professor Doutor Amadeu Soares, meu co-orientador, a oportunidade de integrar o seu grupo de trabalho.

Agradeço à Margarida Corado o seu precioso auxílio durante o trabalho de campo e de identificação de amostras.

Ao Abel Ferreira, agradeço todo o apoio técnico e logístico.

Obrigada às meninas do laboratório das lupas: Liliana, Maria João, Joana M., Joana N., Fátima e Carolina, que partilharam comigo tantos dias no campo e no laboratório e tantas canecas de chá. Por todo o apoio e amizade, e principalmente pela certeza que é do espírito de entreajuda que nascem as soluções.

Obrigada aos meus colegas do LETAL, que partilharam comigo as graças e desgraças de se ser uma aluna de doutoramento.

Obrigada à Juliana, Eliana, Márcia e Marija, por me terem feito sentir em Casa.

Agradeço também, do fundo do coração, a todos os meus amigos, felizmente demasiados para que possa enumera-los um a um. Por terem acreditado mais em mim do que eu própria e por melhorarem tudo com sorrisos e abraços. Um agradecimento especial à Inês, que teve um papel tão importante no início desta aventura e à Cristiana, que me ajudou a terminá-la.

Tenho de agradecer a toda a minha família o seu apoio incondicional ao longo dos anos. Ao meu irmão, aos meus tios e primos, agradeço todos os gestos de bondade e compreensão durante as alturas mais difíceis. Agradeço em especial aos meus pais, o meu porto de abrigo, que sempre me incentivaram a ir e me receberam de braços abertos ao voltar.

palavras-chave

Fogos florestais, ecossistemas lóticos, macroinvertebrados, perturbação, recuperação ecológica, resiliência, diversidade funcional.

resumo

Os efeitos dos fogos nas comunidades lóticas mediterrânicas estão ainda mal documentados. Apesar do progresso verificado nos últimos anos, os dados publicados referem-se principalmente a estudos efetuados na América do Norte, sendo escassa a informação relativa aos rios Europeus. Dada a importância do contexto geográfico regional, quer nos efeitos do fogo no meio ambiente quer na resiliência das comunidades, a lacuna no conhecimento biogeográfico representa uma limitação à implementação de medidas de gestão adequadas.

A presente tese consiste um estudo sistemático dos efeitos do fogo nas comunidades de macroinvertebrados dos ribeiros do Norte e Centro de Portugal. Foi analisada uma cronosequência para averiguar o efeito do fogo numa escala temporal mais alargada (1 a 18 anos) providenciando informação cronológica sobre a recuperação ecológica das comunidades de macroinvertebrados a longo prazo. Os resultados indicaram que as comunidades de macroinvertebrados recuperam em abundância, riqueza taxonómica e em termos de estrutura das comunidades cerca de dois anos após o impacto

Num estudo a curto prazo, em ribeiros recentemente afetados por fogos florestais, foi documentada a resposta inicial dos macroinvertebrados à perturbação pelo fogo e os parâmetros analisados foram comparados com locais de referência onde não ocorreram fogos nos últimos 20 anos. Em todos os períodos amostrados registou-se menor abundância e menor riqueza específica nos ribeiros impactados, bem como diferenças ao nível da estrutura das comunidades entre locais ardidos e os locais de referência.

Tanto no estudo a longo prazo como no estudo a curto prazo, foram avaliados os fatores ambientais que condicionaram a resposta das comunidades biológicas. O tamanho do rio, a extensão da área ardida, condutividade, bem como as características do canal e da vegetação ripária, são determinantes na resposta dos macroinvertebrados ao impacto do fogo, e podem influenciar o grau de susceptibilidade dos ecossistemas lóticos. Foram ainda analisados os resultados dos levantamentos a curto prazo numa abordagem do ponto de vista funcional. Foram analisadas as diferenças ao nível da diversidade funcional e ao nível da frequência das várias características funcionais dos organismos. Foram registadas diferenças pontuais em termos do grupo alimentar e estratégias de reprodução, entre locais ardidos e não ardidos.

Apesar do inequívoco impacto negativo do fogo nas comunidades de macroinvertebrados aquáticos, a recuperação parece ser rápida, demonstrando a sua resiliência perante este tipo de perturbação.

keywords

Wildfires, lotic ecosystems, macroinvertebrates, disturbance, ecological recovery, resilience, functional diversity.

abstract

The effects of wildfires in Mediterranean lotic communities are still poorly documented. Despite some progress in recent years, the published data refer mainly to studies conducted in North America, with little information on European rivers. Given the importance of regional geographic context, both on the effects of fire and on the resilience of the communities, the gap in the biogeographical knowledge represent a limitation to the implementation of appropriate management measures.

This thesis consists in a systematic study of the effects of fire on the macroinvertebrate communities of streams of North and Central Portugal. A chronosequence survey was conducted in order to analyze long-term effects of wildfires (1-18 years) and provide chronological information on the ecological recovery of macroinvertebrate communities. The results indicated that the macroinvertebrate communities recover in abundance and taxa richness and in terms of community structure about two years after the fire impact.

A short-term survey was also carried out, where the initial response of macroinvertebrates to fire disturbance was documented, in streams recently affected by wildfires. The parameters analyzed were compared with reference sites without fire impact for the last 20 years. In all sampling periods, lower abundance and lower species richness were recorded in impacted streams, and differences in community structure were found between burnt sites and reference sites.

In our study, both on long -term and short-term surveys, the environmental features that conditioned the response of biological communities were evaluated. River size, the extent of the burnt area, conductivity, along with channel characteristics and riparian vegetation, were considered determinant in the response of macroinvertebrates communities to fire impact, and can influence the susceptibility of stream ecosystems. We also analyzed the data of the short-term survey on a trait approach. Differences on functional diversity and on frequency of several trait modalities were analyzed. Specific differences in the food group and reproductive strategies between burned and not burned sites were recorded.

Despite the unequivocal negative impact of wildfire on macroinvertebrate communities of Portuguese streams, the recovery seems to be rapid, demonstrating their resilience to this type of disturbance.

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1 General Introduction

1.1 Disturbance concept

Sousa (1984) defined disturbance as “a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established”. White and Pickett (1985) refer to disturbance as any discrete event in time that disrupt the ecosystem, community or population structure and changes resources, substrate availability or the physical environmental. A similar definition was given by Townsend and Hildrew (1994), referring to “any relatively discrete event that removes organisms and opens up space and other resources that can be used by individuals of the same or different species”. Bartha (1997) defined disturbance as “a multi-species, spatiotemporal pattern of mortality of non-competitive origin”. Lake (2000) proposed a definition in which a disturbance occurs when potentially damaging forces are applied to habitat space occupied by a population, community or ecosystems. According to the latter author, the magnitude of the forces may be such that organisms may be killed or displaced, consumable resources (e.g., living space and food) may be depleted and habitat structure may be degraded or destroyed. Resh *et al.* (1988) tried to isolated disturbance from its biotic effects by concentrating in the characteristics of the event itself, and defining disturbance as any event that is not “statistically normal”, i.e., outside the predictable range for a particular environment, in terms of frequency and/or intensity. Various authors also reinforce the need of non-arbitrary criteria to characterize the disturbance regime, for example, by their properties, such as frequency, duration or special extend properties (Rykiel, 1985; Poff, 1992; Lake, 2000).

In addition to defining disturbance, it is also necessary to classify the disturbance process according to its duration. Bender *et al.* (1984) distinguished pulse perturbation as a short-term disturbance that causes a sudden change in the numbers of species from which the assemblage recovers once the disturbance has ceased. A press perturbation was defined as a continuous disturbance causing taxa richness and abundance of species to be permanently changed. The

terms press and pulse are relative to the generation time of the susceptible species (Yount and Niemi, 1990). The main problem with this classification is that it does not differentiate between the cause (the disturbance *per se*) and the effect (the response by the system) of the perturbation, since that response can also be short or long termed. So, Glasby and Underwood (1996), describe 4 types of perturbation according to the temporal pattern of the disturbance and also the response: a discrete pulse and protracted pulse are short term types of disturbances that lead to a short term or to a continued response, respectively. Discrete press and protracted press correspond to continuous disturbances with a short term or a continued response, respectively. For ecological purposes, a discrete press and a discrete pulse are the same, as in both situations the system recovers, whether or not the source of disturbance persists. In addition to pulse and press disturbances, Lake (2000) proposes another form of disturbance to his classification, the ramps, which occur when the strength of a disturbance steadily increases over time (and often simultaneously in spatial scale).

Sutherland (1991) proposed a new classification merely relative to the responses of ecological assemblages to the disturbance. Type I perturbations are the ones where the assemblages resist the disturbance showing no alteration. Type II perturbations cause temporary effects in ecological assemblages while Type III leads to a more permanent shift in the communities.

In summary, disturbance affects the organization of communities and contributes to ecological and evolutionary processes (Yount and Niemi, 1990) and is regarded by many stream ecologists as playing a central role in determining the structure of stream communities (Lake, 2000). In the absence of disturbance, a community is the direct result of competitive, mutualistic and trophic interactions among species.

This work focused on disturbance from the perspective of the response of macroinvertebrate communities to wildfire in terms of impact and recovery, considering parameters such as density, taxa richness and community structure.

1.2 Lotic community's resilience and resistance to disturbance

Recovery is defined by Davis *et al.* (1984) as the process of one or more species returning to "normal" population levels after a disturbance event. It can also be viewed as the reestablishment of community structure to within the range expected over the annual cycle prior to the initial disturbance (Wallace, 1990). Given the difficulties of defining what is a normal (or non-disturbed) state, in which parameters can it be measured or in the cases where the pre-disturbance condition are unknown, recovery is probably best viewed as a return to an ecological state that closely resemble unstressed systems (Gore, 1990).

Post-disturbance populations are attributed the 'strategies' of resistance (enduring the disturbance) and/or resilience (colonizing rapidly following the disturbance) which are related to environmental and ecological parameters (e.g. refugia, dispersal, fecundity) (Lake, 2000).

Similarly, at the ecosystem level, resistance is the capacity of an ecosystem to absorb disturbance and remain largely unchanged, while resilience reflects the ability of an ecosystem to reorganize and return to the pre-condition state following a perturbation, maintaining its essential characteristics in terms of taxonomic composition, structure and function (Holling, 1973; Walker *et al*., 2004).

The ability of stream ecosystems to respond to disturbance and the characterization of the response is linked with both qualities of resistance and resilience (Lake, 2000). Streams are functionally unique in the sense that the downstream movement of water can be viewed as a constant source of instability due to scouring and displacement of material. The response of biota to this environmental constraint includes mechanisms of resilience, like short life-cycles and rapid recolonization in the case of macroinvertebrates, but also resistance, like avoiding disturbance through in-stream retention structures and refugia (Wallace, 1990: Golladay *et al*., 1992).

When compared with other ecosystems, river and stream communities are considered to have a low resistance to disturbance (Reice, 1985; Lake, 2000) but a high resilience (Gurtz and Wallace, 1984; Lake and Doeg, 1985) being able to quickly recover after a disturbance event. The critical difference between lotic communities and communities from other type of habitats appears to reside in the fact that streams are open systems dominated by highly mobile animals and, while community dynamics in other habitats are dominated by population growth through reproduction, community dynamics in streams are dominated by immigration and emigration through drift and dispersal (Death, 2010).

The explanation for quick recovery is provided by the life history characteristics of aquatic organisms (many have short generation times, high fecundity, good dispersal ability) and also the availability of unaffected upstream and downstream areas and other refugia that can promote rapid recolonization of the affect areas (Yount and Niemi, 1990; Milner, 2009). Nevertheless, functional recovery (i.e., abundances, biomass, and production) and taxonomic recovery (individual taxa) may not necessarily happen within the same time frame (Wallace, 1990).

1.3 Fire disturbance on lotic systems

Previous studies provide valuable knowledge on fire-impacted river systems, with ecological effects varying in relation to the three principles: burn intensity and spatial extent of the wildfire; the environmental context (such as the stream size, gradient, precipitation, vegetation, geology, topography, etc); and also the characteristics of the biotic community (species traits, relative isolation of populations, etc).

Scale represents a general damage descriptor that can be respectively applied to the fire (with damage increasing as the area burnt increases) and, inversely, to river size (with smaller, low-order rivers suffering a greater impact that

larger rivers; Minshall, 2003). The effects of fire in small rivers may be further compounded by their general environmental context, with headwater catchments often burning more intensely and completely than larger stream catchments (Minshall *et al*., 1989). Subsequent flooding, channel alteration, sediment transport and sediment deposition are typically more ecologically destructive than the fire itself (Rinne, 1996; Minshall *et al.*, 1997), with the relative position of a site in the river network representing an important determinant of ecosystem recovery (Dunham *et al*, 2003).

From a mechanistic perspective, the impact of fires can be divided into direct effects, occurring at the time of the fire, and indirect effects, occurring over an extended period thereafter (Gresswell, 1999). The fire itself may heat river waters causing high invertebrate mortality (Roby and Azuma, 1995), with small volumes of water, such as first- or second-order streams and shallow, slow-flowing marginal waters of large rivers, being particularly susceptible. Strong peaks in the concentration of nitrate and ammonium may also result from the diffusion of smoke gases, whilst a spike in phosphate can result from the rapid leaching of ash deposited in stream waters (Spencer *et al*, 2003). Fire ash and charcoal deposits from riparian vegetation may also smoother existing food sources (Minshall *et al.*, 2001).

Indirect effects are characterized by subsequent disturbance processes that impact the river habitat. Ash flows can be associated with dramatic changes in water quality, such as an increase in alkalinity and turbidity and a decrease in dissolved oxygen, which impact stream communities (Earl and Blinn, 2003). Precipitation falling on the transformed river basin can represent a major hydrologic disturbance, reducing populations of benthic macroinvertebrates by up to 85-90% (Rinne, 1996). In general, channel stability decreases and habitat features important to macroinvertebrates are often lost (Benda *et al.*, 2003). The loss of terrestrial vegetation is associated with catchment erosion and an increased probability of debris slides depending on slope and precipitation, whilst the increased suspended load and associated sedimentation in the river channel may result in further invertebrate mortalities (Mihuc *et al.*, 1996; Rieman and

Clayton, 1997). Changes in the food web may also be apparent; burnt material appears to be of little dietary importance to river invertebrates (Mihuc and Minshall, 1995; Gama *et al.*, 2007). However, the loss of riparian vegetation reduces detrital inputs to the streams and opens the canopy to solar irradiation causing an increase in autotrophic production (Mihuc and Minshall, 2005).

Studies from North America indicate that lotic ecosystems can be reasonably robust to wildfire disturbance, demonstrating good natural recovery and achieving comparable pre-disturbance levels of taxon richness and abundance within few years, although full recovery may require several decades (Dunham *et al.*, 2007). However, ecosystems that are subject to additional pre- or post-fire impacts may take longer to recovery or experience permanent ecological change. Isolated populations tend to be particularly vulnerable especially where barriers to movement restrict recolonization (Burton, 2005). Additional disturbance to the catchment may further impede recovery with post-fire 'salvage' logging considered to be particularly damaging activity if it is conducted indiscriminately (Karr *et al*., 2004).

1.4 Wildfires in Mediterranean climates and Portugal

Portugal is one of the European countries with largest areas affected by wildfire. Over 2980,000 hectares were burnt between 1990 and 2013 (Figure 1.1 and Figure 1.2, ICNF data).

The Portuguese climate is mostly Mediterranean, characterized by hot, dry summers and cool, wet winters. These climatic conditions, and associated natural vegetation that is resistant to drought and pyrophytic, makes the country prone to wildfires (Nunes *et al.,* 2005).

The fire regime in Portugal has been variable through time and, as in other Mediterranean countries, the annual area burnt has increased significantly in recent decades (Nunes, 2012). Many studies suggest that the increasing

incidence of wildfire in Mediterranean environments can be mainly attributed to the decline of the landscape mosaic that has historically characterized rural areas (Moreira *et al*., 2011). In Portugal, the depopulation of the interior of the country (leading to an increase of unattended scrublands) associated with the increase of fire prone species (especially pine and eucalyptus) and a lack of forest management due to the small average holding size, also contributed this fire increase (Bassi and Kettunen, 2008).

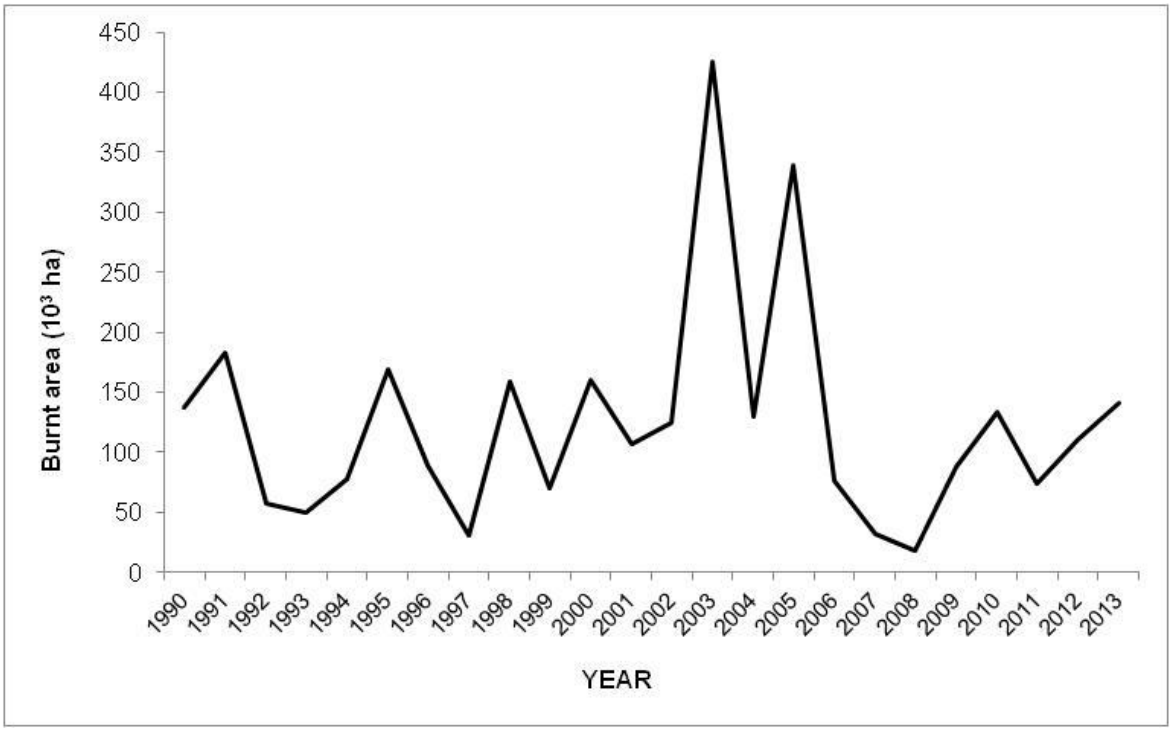

Figure 1.1 – Burnt areas (ha) in Portugal between 1990 and 2013. Data provided by "Instituto da Conservação da Natureza e Florestas", Portugal.

Under global climate change, wildfire is predicted to increase in the Mediterranean Basin. Regional studies for boreal regions suggest an increase in future fire risk (Amiro *et al*., 2009; Flannigan *et al*., 2009; Westerling *et al.,* 2011; Liu *et al*., 2013). Beyond the obvious socioeconomic impact, fire also affects a great range of fundamental ecological processes such as nutrient cycling (Turner

et al., 2007), hydrology and erosion (Shakesby and Doerr, 2006) and influences some important ecosystem characteristics such as biodiversity, biomass, soil characteristics and atmospheric composition (Dube, 2009).

The effects of wildfire on freshwater ecosystems have been documented in recent years for North America (Rugenski and Minshall, 2014) but data from European river systems remains insufficient. The failure to acknowledge the potential damage of fire-impacted catchments in Europe is likely to preclude the implementation of environmentally sensitive post-fire management, thus increasing the risk of further unnecessary impacts to lotic communities, impeding ecological recovery and undermining other efforts of sustainable management.

Whilst fire impact in Portuguese systems remains unknown, current knowledge suggests that wildfires in Portugal are likely to have a major impact on affected river ecosystems. Forested regions in the mountainous interior of central and northern Portugal are characterized by a wet Mediterranean climate with dry summers and wet winters. Water courses are dominated by small, first to fourth order streams with steeply sloping catchments and shallow, stony, hydrophobic soils that are prone to erosion (Shakesby, 2000). Fire frequency peaks during the summer, coinciding with a low hydrograph when ecological communities are naturally stressed. Furthermore, flow regulation and the damming of river channels (associated with small-scale, sustainable agriculture and domestic use), is a widespread practice in rural catchments, these habitat modifications represent an important determinant of macroinvertebrate communities (Monaghan and Soares, 2008) and represent a potential constraint to ecological recovery. The removal of the wood from burnt areas for commercial purposes, a common practice in Portugal, may further delay ecosystem recovery.

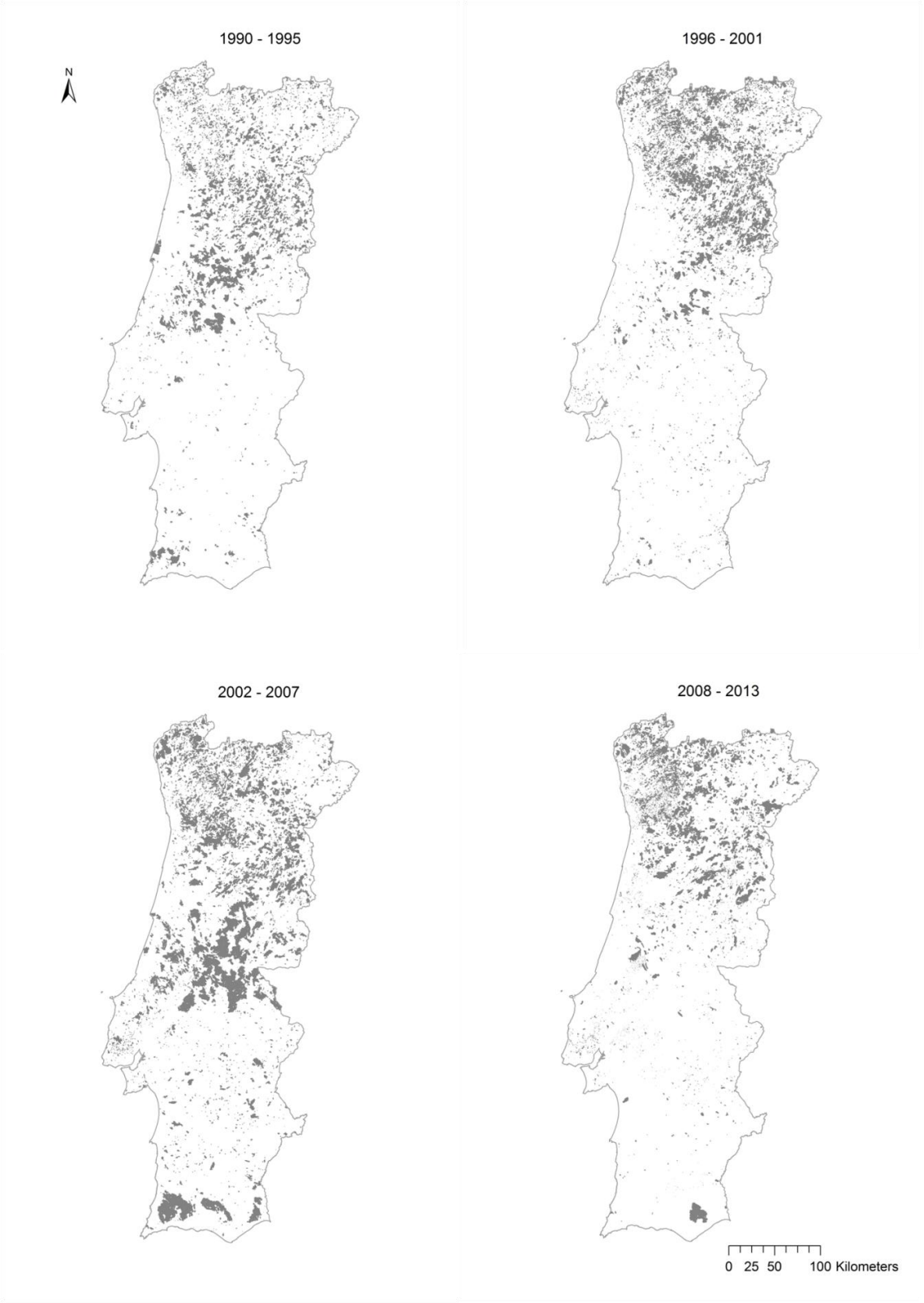

Figure 1.2 – Location of burnt areas in continental Portugal between 1990 and 2013 (Data provided by “Instituto da Conservação da Natureza e Florestas”, Portugal).

1.5 Motivation, objectives and thesis layout

Fire impact on macroinvertebrate communities has been documented from several studies in United States (Arkle *et al*., 2010; Hall and Lombardozzi, 2008; Katsos, 2013; Koetsier *et al*., 2010, Mellon *et al.,* 2008; Minshall *et al*., 1997; Mihuc *et al*., 1996, Rinne, 1996; Roby and Azuma, 1995; Tronstad *et al*., 2011, Viera *et al.*, 2004) including mid/long-term studies that elucidate recovery mechanisms (Minshall *et al*., 2001; Mihuc and Minshall, 2005; Rugenski and Minshall, 2014; Robinson *et al*., 2005).

From other prone-fire regions of the world, knowledge is still very scarce (Verkaik *et al*., 2013a for macroinvertebrate communities in NE Spain; Reid and Thoms, 2012 and Verkaik *et al*., 2013b for Australian streams). For Portugal, despite being one of the countries of European Mediterranean region most affected by fire, there is still no data on the effects of fire on lotic macroinvertebrate communities. The main goal of this work was to document the response of macroinvertebrate communities to fire impact over short and long term timescales. the specific objectives where:

1. To document the response of macroinvertebrate community organisation to fire-impacted catchments.

2. To describe ecological recovery following forest fire.

3. To describe habitat changes associated with fire-impacted rivers and how they affect macroinvertebrate communities' response to fire impact.

4. To understand the mechanistic processes associated with fire-induced degradation.

5. To contribute to knowledge for river restoration and enhanced ecological recovery.

This thesis is organized in five chapters: (1) a general introduction, exploring the main concepts related to the subject of this thesis; (2) a chapter named “Mid-term effects of wildfire on macroinvertebrate communities (a chronosequence survey) in North and Central Portugal” describing fire impact and recovery on macroinvertebrate communities in mid/long-term; (3) a chapter entitled “Short-term effects of wildfire on macroinvertebrate communities of North and Central Portugal”, where short-term macroinvertebrate responses to fire impact are documented, as well as the habitat features that mediate that response (4) a chapter on “The impact of wildfire on functional composition and structure of macroinvertebrate communities”, where a trait-based approach is applied; and (5) a concluding remarks chapter, summarizing the main findings . All the references used are listed in the end of the respective chapter in a specific section.

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2 Mid-term effects of wildfire on macroinvertebrate communities (a chronosequence survey) in North and Central Portugal

2.1 Introduction

Fire plays an important role in community composition and species distribution patterns (Bond and Keeley, 2005; Bowman *et al.*, 2009). Over an evolutionary time-scale, it selects for traits that maximize survival and post-fire proliferation (Pausas and Keeley, 2009); over an ecological time scale fire shapes the structure and function of fire-adapted communities (Bond and Keeley, 2005). With hot, dry summers Mediterranean climatic zones are fire-prone; while their terrestrial fauna and flora recover rapidly from fire disturbance (Naveh, 1975; Moretti *et al*., 2009; Elia *et al*., 2011; Pausas and Paula, 2012), little is known about the effects on lotic Mediterranean ecosystems (Gasith and Resh, 1999; Verkaik *et al*., 2013).

According to Minshall (2003), the effects of fire disturbance can be divided into direct effects and indirect effects. Direct effects are limited to the time of the fire and extend to the first major precipitation runoff event. Indirect effects begin with the first runoff following fire and continue over an extended period of time and are often associated with increased erosion. In addition, there are likely to be longer-term alterations associated with the removal and eventual successional replacement of the riparian cover and consequent alteration of food webs (Minshall *et al*., 1989).

Direct effects of fire disturbance include increases in water temperature that tend to be more pronounced in shallow streams and small volumes of water (Minshall, 2003). High concentration of nitrate and ammonium from smoke diffusion and phosphate peaks from ashes leaching (Spencer *et al*., 2003) may also occur. Changes in water quality can also be caused by ash input resulting in an increase in alkalinity and turbidity and a decrease in dissolved oxygen, (Earl and Blinn, 2003).

Minshall (2003) considered the indirect impact of fire to be more ecologically damaging when compared to the direct effects. The loss of terrestrial vegetation increases catchment erosion. As eroded material is washed into river

systems it can cause both scour and deposition in stream channels, depending on the amount of precipitation and catchment slope (Wondzell and King, 2003). In addition, post-fire erosion and floods can transport large volumes of burnt wood into the streams causing severe modifications and decreasing channel stability (Benda *et al*., 2003; Vaz *et al*., 2011; Vaz *et al*., 2013).

Several works registered decreases in abundance and taxa richness of benthic macroinvertebrates in fire-impacted streams (Minshall *et al*., 1997 and 2001; Richards and Minshall, 1992; Earl and Blinn, 2003; Vieira *et al*., 2004). For these organisms, the most drastic effects result from flooding and mass movement of eroded top-soil after rainfall events that can reduce the populations by up to 90% (Rinne, 1996). In addition, changes in species dominance and community composition can occur. Changes in community structure can remain even after the recovery of general parameters, such as density and diversity (Roby and Azura, 1995; Vieira *et al*., 2004; Mellon *et al*., 2008). The loss of riparian vegetation can increase primary productivity due to increased sunlight with open canopy riparian vegetation, which together with the resulting decrease in leaf litter input, may cause a shift in food webs from allochthonous to autochthonous food sources (Spencer *et al*., 2003; Mihuc and Minshall, 2005).

Post-fire succession depends on species traits, geographic barriers to colonization and the hydrologic conditions in the years following the fire impact. Initial assemblages are usually dominated by taxa with strong larval and adult dispersal ability (Vieira *et al*., 2004; Vieira *et al*., 2011). In addition, post-fire communities are often dominated by generalist feeders (Mihuc and Minshall, 1995; Vieira *et al*., 2004; Malison and Baxter, 2010). Recovery after a wildfire can be especially sensitive to the extent to which riparian area and floodplain remains intact (Minshall, 2003). Additional disturbance caused by poor post-fire management practices, like salvage logging, can also delay the recovery process (Gresswell, 1999; Minshall, 2003). In any disturbance event, the presence of undisturbed upstream area or terrestrial refugia that can act as source areas that can promote rapid recolonization and accelerate the recovery rates (Gore, 1990; Townsend and Hildrew, 1994). Numerous studies have reported that

macroinvertebrate communities achieve levels of abundance and diversity comparable to pre-disturbance levels within one to ten years (Richard and Minshall, 1992; Robinson *et al*., 2000; Minshall *et al.,* 2001; Earl and Blinn, 2003).

In a chronosequence survey spatially discrete sites that have been impacted at different times in the past provide discrete examples of ecological recovery over different time-scales, thus by substituting space for time a chronosequence survey provides insight to the temporal phenomena of ecological succession (Pickett, 1989). This experimental design provides the opportunity to study ecological processes over an extended time period that may not be otherwise feasible by direct observation (Walker *et al*., 2010). In the present work, a chronosequence was used to investigate the impact and recovery of macroinvertebrate communities from upland streams impacted by fire disturbance in North and Central Portugal over a 18 years period, in order to assess: 1) the impact and the recovery in terms of macroinvertebrate abundance; 2) taxa richness; 3) community structure, i.e., secondary succession following fire and 4) the importance of habitat features in mediating the impact/recovery process.

2.2 Methods

2.2.1 Study Area

The present study focused on low order, upland headwater streams in North and Central Portugal. Land use was dominated by Pine and/or Eucalyptus plantations, being substituted by heathland and shrubland at higher altitudes.

Data from wildfires occurring between 1990 and 2007, provided by the national forest authorities ("Autoridade Florestal Nacional"), were incorporated in a GIS database along with other map derived geographic information. This information served as the basis for the selection of 15 study sites (Figure 2.1; Table 2.1), representing a chronosequence of catchments that were impacted by wildfire 18, 15, 13, 10, 7, 6, 5, 3, 2 (3x) and 1 (4x) year(s) priori to 2008. The main selection criteria were that over 90% of the catchment was impacted by the wildfire

with minimal potential impacts from human activities (i.e. negligible urban, industrial or agriculture impacts).

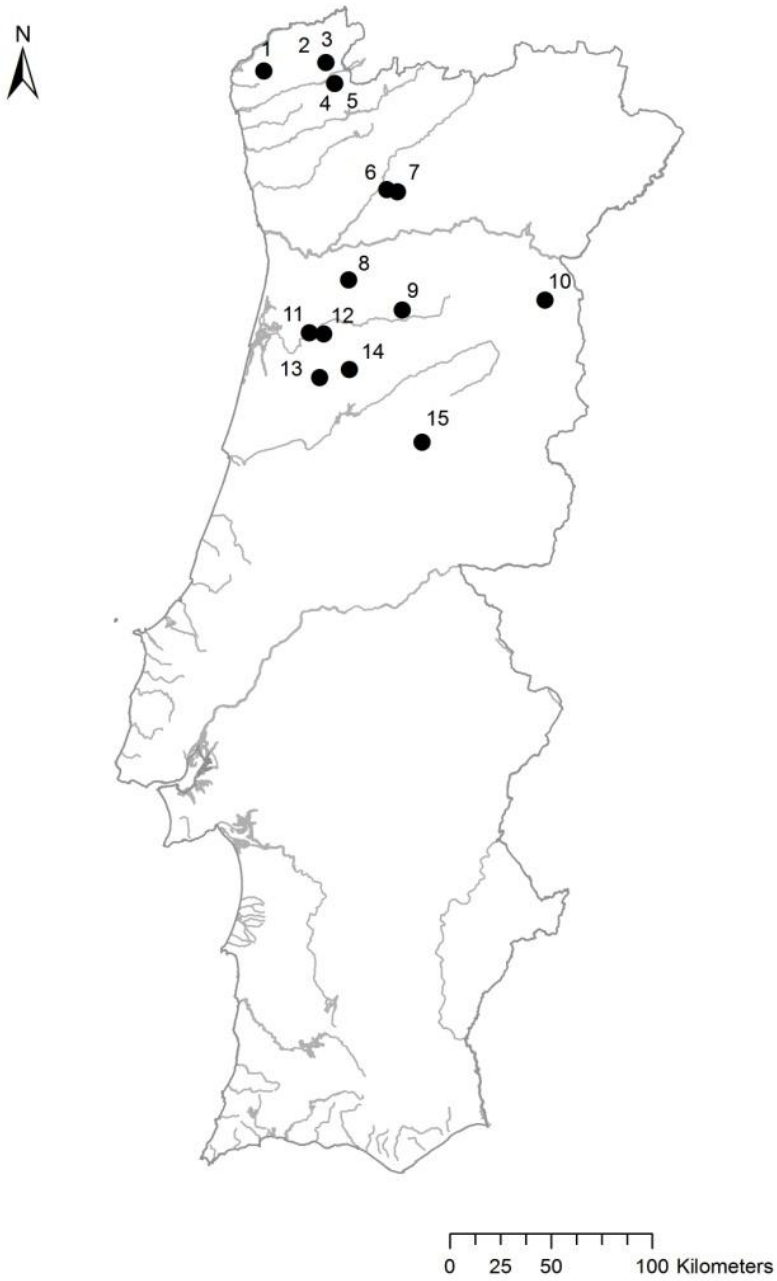

Figure 2.1 – Sampling sites: 1 Covas (burnt in 1993); 2 Bouça Donas A (2006); 3 Bouça Donas B (2006); 4 Ermida A (2007); 5 Ermida B (2007); 6 Ribeira das Víboras (2007); 7 Pardelhas (2007); 8 Paradinha (2002); 9 Água d'Alte (1998); 10 Penha d'Águia (2003); 11 Vila Nova de Fusos (1995); 12 Carrazedo (2006); 13 Boialvo (2005); 14 Múceres (1990); 15 Sobral de S. Miguel (2001).

Table 2.1 - Summary of the environmental variables at catchment scale (range) of the study sites

Variable (units)	Range
Catchment area (ha)	42.8 – 639.95
Burnt area (% catchment)	90 – 100
Altitude (meters)	50 – 790
Stream Link Magnitude	3 – 44
Slope (meters)	30 – 310
Forest area (%)	0 – 100
Shrubland area (%)	0 - 100
Agriculture areas (%)	0 - 19

Forest area = catchment percentage occupied by forest cover (eucalyptus and pine plantation, deciduous or mixed forest).

2.2.2 Sampling Surveys

Ecological surveys were conducted during August and September 2008. Macroinvertebrates were collected by kick-sampling riffle habitats and kick and sweep sampling of slow-flowing habitats and submerged vegetation and woody debris, using a 500 micrometer mesh pond net. Sampling effort was divided between riffles (2 minutes sampling), pools (1 minute) and water column substrates (wood, tree roots and/or macrophytes; 1 minute). Samples were preserved separately by habitat type in 70% ethanol. In the laboratory macroinvertebrates were separated from organic and mineral material in a white tray, under strong light. Macroinvertebrates were identified to species/genus level using a binocular microscope, with the exception of Chironomidae (tribe), Arachnida (family), Annelida (class) and Turbellaria (class).

Stream habitat was characterized using a modified version of RHS (River Habitat Survey), adapted to Portuguese up-land streams (Monaghan and Soares, 2008); observations and measurements were carried out at 10 “spot-check” points, spaced at 20 meter intervals over a 200 meter length of the stream where macroinvertebrate samples were collected. At each spot-check key bank and channel features such as bank height, substrate, flow type, aquatic vegetation,

cover and human modifications were recorded. Characteristics of the riparian corridor, including shade and vegetation complexity were also registered (Raven *et al*., 1998). A more detailed complementary description of macroinvertebrate microhabitat, in terms of substrate size, was made at macroinvertebrate sampling locations. Water quality parameters including pH, conductivity, dissolved oxygen and temperature were measured, *in situ*, using portable meters and water samples were collected for laboratory analysis of nitrogen (N), ammonia (NH_4^+), nitrates (NO_3^-), nitrites (NO_2^-), hydrogen cyanide (HCN), total phosphorus (total P), soluble reactive phosphorus (sol P), dissolved silica (Si), chloride (Cl^-) and sulphate (SO_4^2) concentrations.

2.2.3 Data Analysis

Macroinvertebrate samples were pooled (combining riffle, pool and water column samples).

Sites physical characteristics described by habitat surveys were reduced by PCA to provide a summarized gradient of habitat change across sites. Habitat features were divided in descriptors of channel, banks and riparian zone and described by separate ordinations. Ordination scores were used to characterize individual streams based on the site's centroid in ordination space. Management intervention in bank structure represented by reinforced, walled banks was widespread; the overall extent of bank-modifications was expressed as a ratio between spot-checks with walls and spot-checks without walls; walls adjacent to the wetted channel given a score of 2 and wall set-back from the wetted channel (that presumably reduces their ecological impact) scoring 1.

Data from chemical analysis of water samples were reduced by PCA and the scores of the two first axes were used as general summaries of water quality.In this study, Bray-Curtis dissimilarity was used to calculate distance between biological assemblages. This coefficient is an asymmetrical quantitative measure that excludes double zeros, that makes it suitable for ecological data

(Legendre and Legendre, 2012). This measure scales from zero to one, with zero representing samples with the same composition and one representing sites with no taxa in common (Bray and Curtis, 1957).

Non-metric multidimensional scaling (NMDS) was used to represent the similarities between macroinvertebrate community structure between sampling sites. NMDS is a robust ordination technique for the analysis of community data, when the aim is to recover the compositional dimensions associated with underlying environmental gradients (Minchin, 1987). Another advantage of NMDS ordination is the fact that this method is not limited to a specific resemblance measure (Clarke *et al*., 2006).

To reduce the relative importance of dominant species analysis was based on logarithm transformed abundance data (Lepš and Šmilauer, 2003). Species with incidence and abundance lower than two were exclude from the analysis, in order to diminish the the influence of rare occurrences which can distort ecological meaning (Cao and Larsen, 2001). Groups of samples with higher similarity were defined by Cluster Analysis (Group Average Linkage).

To determine which taxa provides higher discrimination between those clusters a SIMPER (Similarity Percentage Analysis) was performed (Clarke, 1993).

Vector-fitting analysis (R vegan package; Okasen, 2012) was used to examine the correlation between environmental variables and ordination of biological data provided by the NMDS analysis. The correlation identifies the variables contributing most to the observed ordination pattern of the macroinvertebrate communities.

All the analysis were performed on R software, except SIMPER that were performed on PRIMER 6.

2.3 Results

2.3.1 Physical habitat

The first two ordination axes of channel characteristics explained 47.2% of the total variation. The first axis (Channel-1) represented 26.3% of the variation and described a transition from streams with large substrate and a higher percentage of in-stream cover, where moss was the predominant vegetation to streams with smaller substrate where in-stream vascular plants were more common and an increased occurrence of submerged macrophytes is observed (Table 2). The second axis, Channel-2 (20.9%) described a gradient of flow characteristics and depth, ranging from shallow, rapid streams to deeper and slower flowing streams.

The primary axis of bank features (Bank-1) explained 38.2% describing a trend from, narrow streams with low banks of small substrate size to wider streams, with high banks and larger bank material. Bank-2 (16.6%) ranged from sites with eroding undercuts to sites with material deposition associated with sidebars and middle channel bars (Table 2.2).

Primary variation in riparian vegetation (Riparian-1) captured 46.6% of the global variation and described a decrease in complexity (from broadleaf woodland, and eucalyptus/pine plantations to grasslands or pastures) and decreasing shade.

Variation in water quality along the primary axis (43.9%) was mostly explained by the decrease of Silica and Chloride and the increase in nitrates, total Nitrogen and sulphates (Water-1; 43.9%).

Table 2.2 - Summary of principal component axis based on PCA of habitat features (channel, bank, riparian zone and water quality). Values indicate the percentage variance explained by each variable.

Channel-1	Channel-2	Bank-1	Bank-2	Riparian-1	Water-1
Substrate -0.81	Flow -0.68	Right height 0.80	Undercuts -0.74	Right 1meter complexity -0.83	Chloride -0.80
Moss -0.60	Depth 0.89	Left height 0.78	Sidebars 0.72	Right face complexity -0.82	Dissolved Silica -0.70
In-stream cover -0.41		Width 0.70		Left face complexity -0.81	Sulphates 0.41
Vascular Plants 0.25		Right material 0.65		Left 1meter complexity -0.80	Nitrogen 0.45
Submerged terrestrial vegetation 0.48		Left material 0.60		Right 5meters complexity -0.70	Nitrates 0.83
				Left 5meters complexity -0.55	
				Tree shade -0.52	
				Herbaceous shade -0.04	

2.3.2 Biological data

Globally, 195 taxa were distinguished, mostly belonging to Insecta(92%). Diptera was the most abundant order, representing 46.6% of the total of individuals > Trichoptera (10.7%) > Plecoptera (10.3%) > Coleoptera (10.1%) > Ephemeroptera (9.9%) > Odonata (8.6%) > non-insect taxa (3.2%) > Megaloptera (0.3%) and Heteroptera (0.3%).

Taxa richness varied between 29 (one year after fire) and 85 (10 years after). Total abundance varied between 238 (1 year) and 3017 individuals (15 years). Visual inspection of taxa richness (Figure 2.2) and total abundance (Figure 2.3) indicated discernible impact for the first two years, revealing significantly lower values when samples were pooled (years 1-2 vs. years 3-18; richness, $F_{1,13}$=8.456; p=0.012; abundance, $F_{1,13}$=16.698; p=0.001). Recovery in both taxa richness and abundance were best described by a logarithmic relationship with time (r^2 for taxa richness = 0.4528, p=0.006; and r^2 for total abundance = 0.595, p=0.001).

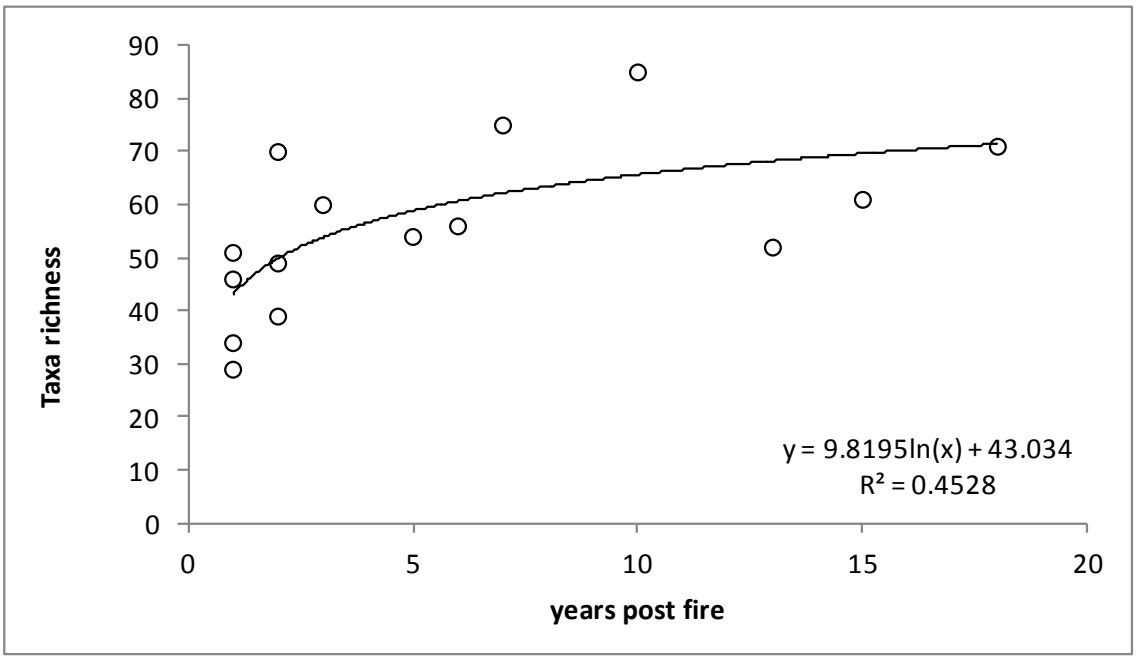

Figure 2.2 – Taxa richness versus years since fire

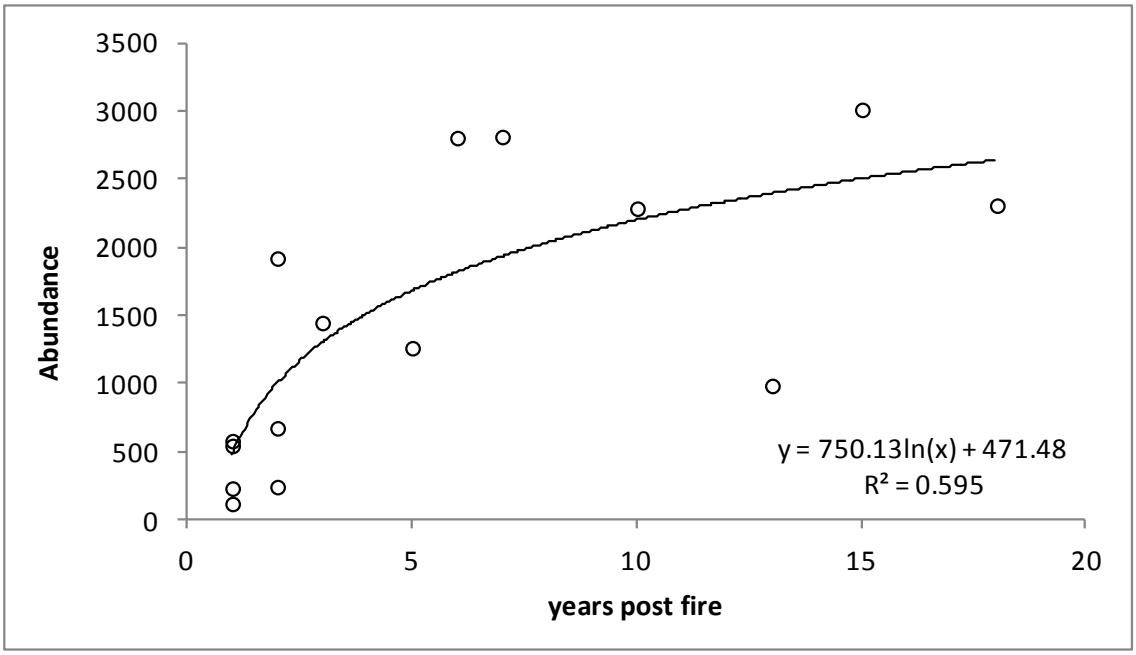

Figure 2.3 – Abundance versus years since fire

Classification distinguished three community types, representing 45% level of Bray-Curtis similarity (figure 2.4, upper). The first group (A), in the negative part of NMDS1 axis, was associated with higher diversity and abundances and is composed by the sites that burned longer ago, along with one point burned in 2006 (2 years previously). Those sites are characterized by higher percentage of macroinvertebrates of slow growth and larger size, such as Odonata and Trichoptera and high abundances of Chironomidae (figure 2.5). Group B, composed of two sites that burned in 2006 and two sites that burnt in 2007, with fewer Odonata and Thricoptera and a higher percentage of Ephemeroptera. Group C, (2007 fires) show low abundance and diversity and was characterized by very low richness of common macroinvertebrates representative of various orders such as *Habrophlebia* sp., *Hexatoma* sp., *Centroptilum* sp. or *Simulium* sp..

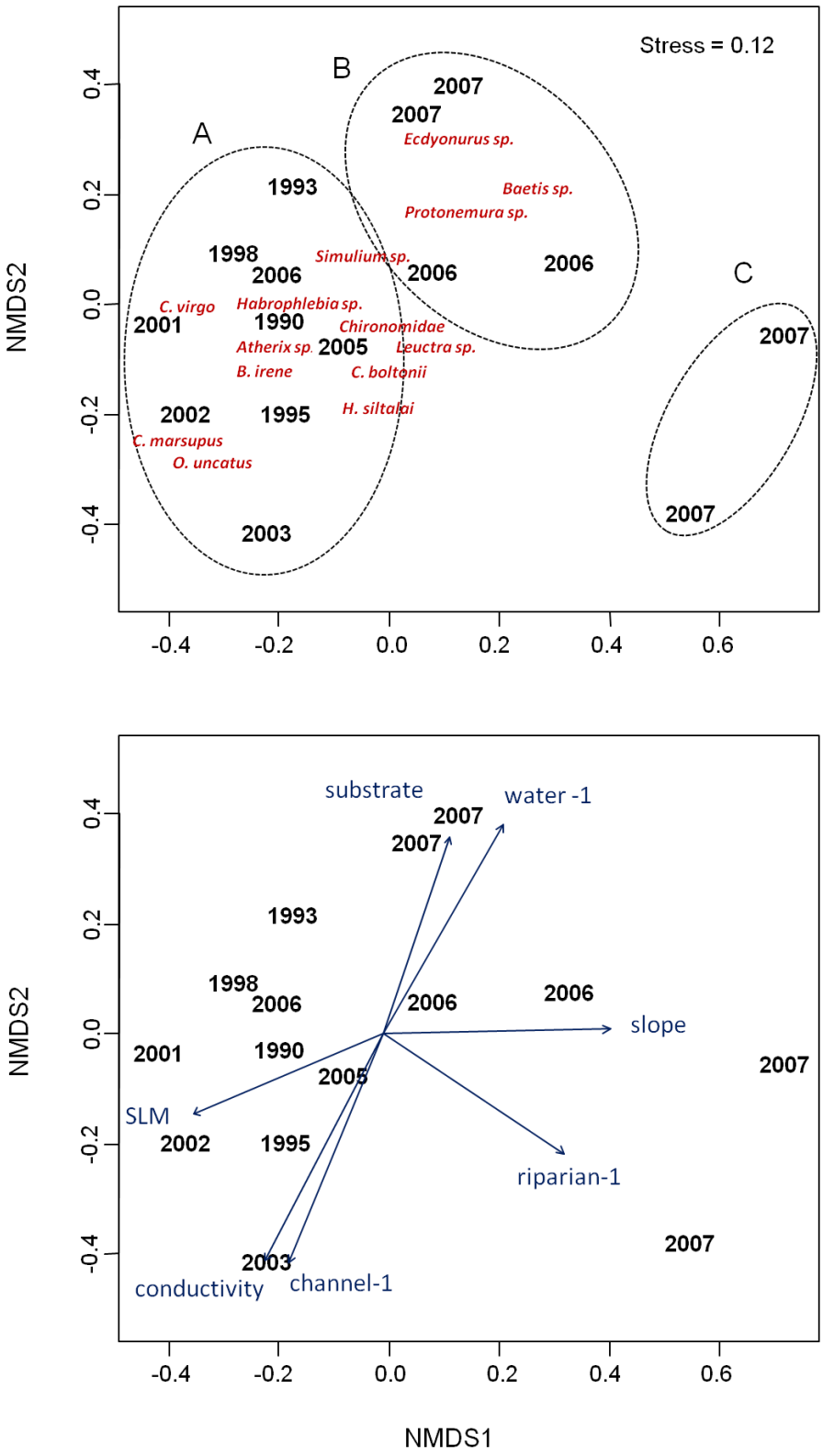

Figure 2.4 – NMDS of the macroinvertebrate communities based on Bray-Curtis resemblance matrix, showing groups with 45% level of similarity and respective most discriminant taxa (upper) and correlated environmental variables with vector fitting (bottom).

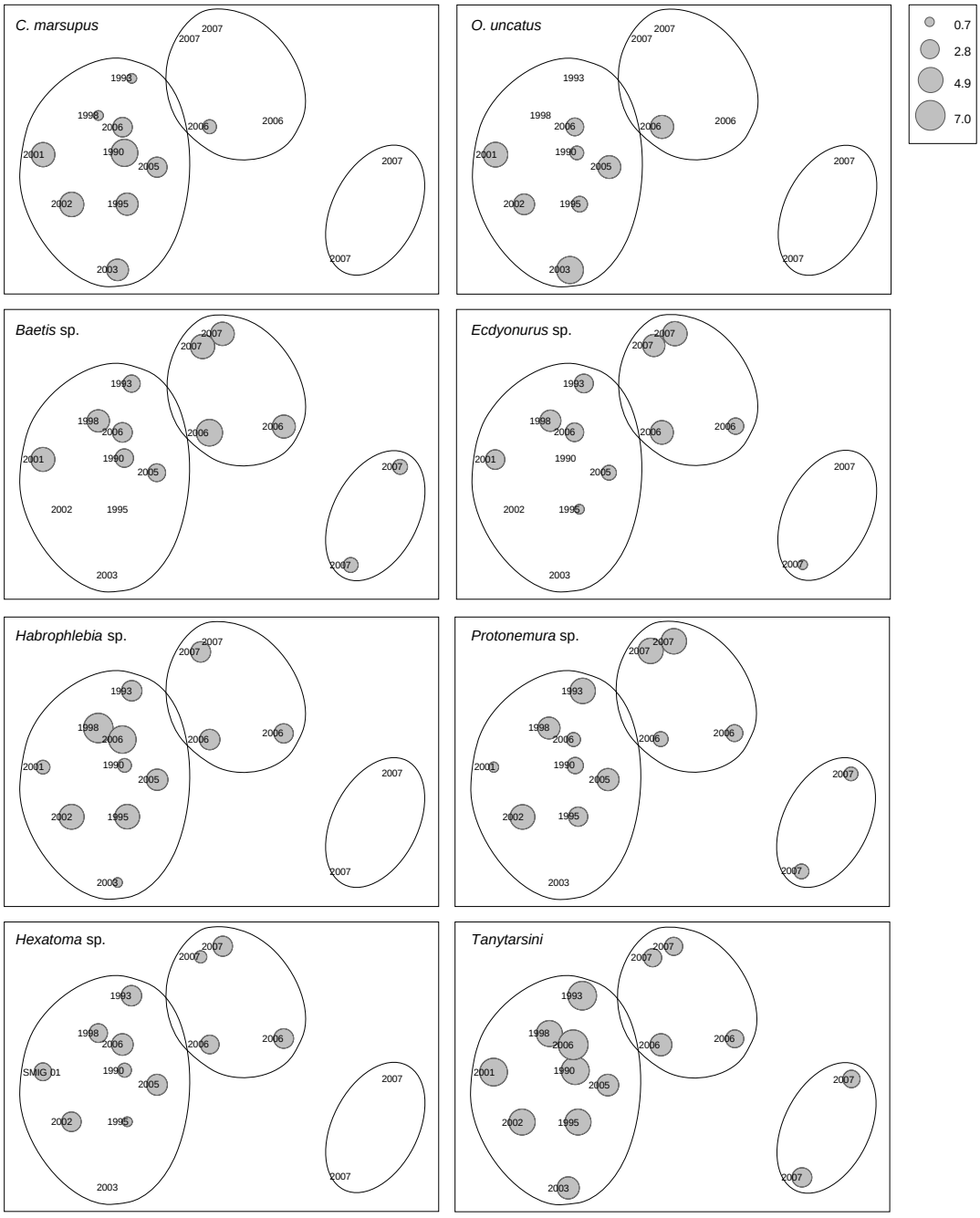

Figure 2.5 – NMDS of the macroinvertebrate communities based on Bray-Curtis resemblance matrix, showing groups with 45% level of similarity representing the abundance (log transformed data) of most some of the most discriminant taxa: *Camaloceras marsupus*, *Onychogomphus uncatus*, *Baetis* sp., *Ecdyonurus* sp., *Habrophlebia* sp., *Protonemura* sp., *Hexatoma* sp., *Tanytarsini*

2.3.3 Relationship between biological data and environmental data

The correlation between the results of the ordination of biological data and the environmental variables are summarized in Table 2.3.

Habitat variables defined at the site scale were identified as the major determinant of the macroinvertebrate community structure. Substrate size, conductivity and water quality were significantly correlated with biological data. At the reach scale, the structure of the channel and the riparian vegetation were correlated; at catchment scale, slope and stream link magnitude were correlated (Table 2.3).

Recently burned sites differed in relation to the environmental parameters. Group B (on the positive side of NMDS2 axis) was correlated with larger mean substrate size, channel vegetation dominated by moss and a higher percentage of in-stream cover. Group C was associated with channels dominated by macrophytes and/or submerged vegetation, but with less in-stream cover and less complex riparian vegetation (Figure 2.4, bottom).

Recently impacted sites (< 2 years) showed significant differences in relation to Water-1, with higher concentrations of sulphates, nitrates and total nitrogen ($F=1.278$, $p<0.005$).

Table 2.3 – Correlation coefficients and significance levels between NMDS ordination of biological data and environmental variables measured at site, reach and catchment scale. Significant p-values are indicated by * for 0.1 significance level, ** for 0.05 significance level and *** 0.01 based on 999 permutation test

Environmental variables	R^2 (p-value)
Site scale	
Substrate size	**0.4117 (0.042) ***
Conductivity	**0.6002 (0.001) *****
Temperature	0.3597 (0.065)
Water-1	**0.5496 (0.010) ****
Reach scale	
Channel-1	**0.5823 (0.005) ****
Channel-2	0.2889 (0.126)
Bank-1	0.3439 (0.073)
Bank-2	0.0947 (0.530)
Riparian-1	**0.4426 (0.031) ***
Embankment	0.0644 (0.682)
Catchment scale	
Forest	0.0428 (0.770)
Slope	**0.4850 (0.020)***
Altitude	0.2553 (0.172)
Link Magnitude	**0.4042 (0.046)***
Time	
Years post fire	0.3072 (0.110)

2.4 Discussion

2.4.1 Effects of fire on abundance in richness and abundance

Recently burnt sites (2006 and 2007) showed lower taxa richness and abundance but sites burned previously (> 2 year) seemed to demonstrate recovery. These results are consistent with several studies on North American streams, that documented recovery times between one to four years (Table 2.4).

Several authors (Minshall *et al*., 2001; Vieira *et al.,* 2004; Arkle *et al*., 2010) state that community composition takes longer to recover than simplistic community parameters such taxa richness or abundance. Food web alterations, such as higher percentage of generalist feeders, are some of the changes highlighted by these studies that can last more than 10 years (Vieira *et al.,* 2004; Mihuc and Minshall, 2005). In this study, the communities appeared to recover within two years even in terms of its structure.

2.4.2 Effects on macroinvertebrate community structure

In this study, the macroinvertebrate taxa that appeared to be most affected by fire impact were Odonata e Trichoptera. These taxa are characterized by their larger size, associated with slow growth and longer life cycles and were absent from recently burnt sites. Other taxa shown sensitivity to fire disturbance, such blackflies, craneflies and mayfly from the *Habrophlebia* genera. Others studies state the sensitivity of Siimulidae and some Ephemeroptera to physical disturbances that are typically associated with fire disturbance, such as flooding (Matthaei *et al.*, 1997; Milner *et al.,* 2012), sediment depositions (Rabení *et al*., 2005) or logging (Ely and Wallace, 2010).

Despite the low abundance or absence of these larger macroinvertebrates, some sites supported a high abundance of mayflies, e.g. *Baetis* sp. and *Ecdyonurus* sp. These taxa, despite being less tolerant to sediment disturbance (Rabení *et al*., 2005; Larsen *et al.*, 2011), might be re-colonizing fire impacted streams after one or two years. A rapid increase in numbers of these mayfly genera following a physical disturbance is a common occurrence (Gurtz and Wallace, 1984; Bradt *et al.*, 1990; Anderson, 1992; Zueling *et al*., 2002; Vieira *et al.,* 2004; Li *et al.,* 2012), including fire disturbance (Rugenski and Minshall, 2014) and can be explain by their generalist feeding habits, short generation times and high fecundity (Tachet *et al.*, 2000).

The effects of wildfire on lotic systems and the recovery times of aquatic communities can be variable, depending on the resistance and/or resilience of

present taxa (Hall and Lombardozzi, 2008) and on several abiotic factors. The severity of post-fire impacts such as sediment loading (Earl and Blinn, 2003; Vieira *et al.*, 2004; Mellon *et al.*, 2008), water quality degradation (Rinne, 1996; Hall and Lombardozzi, 2008), channel modification (Minshall *et al*., 1997, Mihuc and Minshall, 2005) and reduced riparian cover (Arkle *et al*., 2010) can delay the recovery process.

2.4.3 The influence of environmental variables on fire impact

In terms of environmental variables that may affect the degree of impact and/or recovery of macroinvertebrate communities from wildfire at the site scale, substrate size, conductivity and water quality seems to have an important role. Streams with more coarse and stable substrate suffer fewer disturbances during flood events and present more possibility of refugia from where macroinvertebrate re-colonization can occur (Rempel et al., 1999; Hussain and Pandit, 2012). Consequently, communities from sites with larger substrate size and more in-stream cover tend to be less sensitive to hydrologic disturbances associated with post-fire erosion and flood. In terms of water quality, the increase of nutrients such as nitrates and sulphates in burnt catchments has been described in several studies (Britton, 1991, Gerla and Galloway, 1998; Earl and Blinn, 2003; Lane *et al*., 2008; Rhoades *et al*., 2011; Smith *et al*., 2011, 2012) including for Pine and Eucalyptus plantations in Central Portugal (Thomas *et al*., 2000a; Thomas *et al*., 2000b; Ferreira *et al*., 2005). In our study, the higher concentration of nitrates and sulphates in recently burnt sites was not followed by higher water conductivity levels (a similar result to that obtained by Hall and Lombardozzi, 2008). Along with hydrological physical perturbation, nutrient input can also be responsible for the lower taxa richness and abundance in recent fire-impacted sites, since it can cause the decrease of oxygen availability and consequently the reduction of water quality sensitive taxa, with higher oxygen requirements such as Ephemeroptera (except Baetidae), Plecoptera, Trichoptera, (Lemly, 1982; Camargo *et al*., 2004; Wang *et al*., 2007).

At the reach scale, channel and riparian vegetation structure were correlated with the inferred gradient of ecological impact-recovery. The group of sites most affected by fire impact presented less complex riparian vegetation, while recently burnt sites where a complex riparian structure resisted fire disturbance appeared to suffer less impact and/or recovered more rapidly. This suggests that complex riparian vegetation can mitigate the effects of post-fire erosion. Riparian zones can also act as a buffer and work as a refuge for fire-sensitive species that can quickly re-colonize the affected stream (Dwire and Kauffman, 2003; Petit and Naiman, 20007). Channel cover and stream vegetation also appeared to be an important determinant of resilience/recovery. Mosses acts not only as substratum, providing refugia and a complex and stable habitat but it also accumulates large quantities of periphyton and detritus that can be used as food source (Suren, 1991).

At the catchment scale, slope and stream size seems to play an important role with smaller catchments with steeper slopes more prone to fire impact because it increases sediment transport and deposition (Rinne, 1996; Minshal *et al.,*1997).

2.5 Conclusion

In conclusion, results indicated the rapid recovery of macroinvertebrate communities - within two years after fire impact - in terms of taxa richness and abundance. The impact-recovery process was influenced by the environmental context at catchment scale (slope and stream size), reach scale (channel features and riparian vegetation) and at site scale (substrate size, conductivity, water quality parameters).

Table 2.4 – Summary of studies indicating the recovery times of macroinvertebrate communities from fire impact (*BACI = Before-After Control-Impact Design)

Authors	**Study design**	**Study time scale**	**Location**	**Recovery in taxa richess**	**Recovery in abundance/density**	**Other observed impacts**
Richards & Minshall (1992)	5 burnt streams + 5 references (low order)	5 years	Salmon River, Idaho (USA)	4 years	?	No recovery on community structure
Roby & Azuma (1995)	1 burnt streams + 1 references (low order)	11 years	Northern California (USA)	3 years	1 year (density even increase)	Lower but very variable Shannon Diversity Index in burnt site
Rinne (1996)	3 headwaters (BACI design)	3 years	Tonto National Forest, Arizona (USA)	No recovery	No recovery	
Minshall *et al.* (1997)	18 burnt streams + 3 references (low order)	4 years	Yellowstone National Park, Idaho (USA)	1 year	1 year	No recovery in terms of c community composition
Minshall *et al.* 2001	6 burnt streams + 1 reference (low order)	10 years	Yellowstone National Park, Idaho (USA)	More variation than reference	More variation than in reference site	More variation in community composition during all period
Earl & Blinn (2003)	5 points in the same river	5 years	Gila River, New Mexico (USA)	?	1 year	No trends observed (undifferentiated impacts in the entire community)
Spencer *et al.* (2003)	2 reaches (burnt and not burnt area in each)	5 years	Glacier National Park, Montana (USA)			Change to autochthonous food sources in burnt sites through the 5 year period
Vieira *et al.* (2004)	1 burnt stream (BACI* design) + 1 reference stream	6 years (post fire)	North Central New Mexico (USA)	4 years	1 year	Community composition changes; higher generalists percentage (no recovery after 6 years)
Mihuc & Minshall (2005)	2 burnt streams + 2 references (low order)	10 years	Yellowstone National Park, Idaho (USA)	?	?	Food webs alterations (no recovery in 10 years)
Hall & Lombardozzi (2008)	6 burnt streams + 7 references (low order)	2 years	Pike-San Isabel National Forests, Colorado (USA)	2 years	No recovery	
Mellon *et al.* (2008)	5 burnt streams + 5 references (low order)	2 years	Colville National Forest, Washington (USA)	?	?	Changes in the assemblages composition, differences in dominance (no recovery)
Arkle *et al*. (2010)	6 burnt streams + 7 references (low order)	4 years	Payette National Forest Idaho, USA	?	More variation on burnt streams	Changes in community structure and composition (no recovery)
Malison & Baxter (2010)	9 burnt streams + 3 references (low order)	5 years	Payette National Forest, Idaho, USA	?	?	Changes in the assemblages composition, more generalist feeders(no recovery)
Tronstad *et al*. (2010)	1 stream (BACI* design)	2 years (post-fire)	Yellowstone National Park, Idaho USA	No differences	2 years (density increase in 2nd year)	More generalists

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3 Short-term effects of wildfire on macroinvertebrate communities of North and Central Portugal

3.1 Introduction

Wildfire is an important process that shapes and influences the function and structure of landscapes, ecosystems and biological communities worldwide (Pausas and Schwilk, 2012). The Mediterranean Basin is recognized as a fire prone region: climatic factors (strong seasonality, with warm dry summers and large variability in rainfall) combined with anthropogenic factors make fire disturbance fairly common (Gasith & Resh, 1999; Keeley *et al.*, 2012). Although most Mediterranean aquatic ecosystems may be fire-adapted and show rapid recovery, systems with low connectivity, with some source of anthropogenic disturbance or inappropriate post-fire management can be more sensitive to the effects of wildfire (Gasith & Resh, 1999; Gresswell, 1999). In lotic systems, the most severe impacts are usually associated with increased erosion and sediment inputs, transport, and deposition after wildfire occurrence (Minshall, 2003). The disturbance following these hydrologic and geomorphologic changes are often accompanied by changes in water chemistry, channel morphology and in-stream habitat (Shakesby and Doerr, 2006; Verkaik *et al*., 2013a). Several studies have shown biotic responses to these disturbances, such as reduction in abundance, taxa richness and changes in community composition (Rinne, 1996, Earl and Blinn, 2003; Vieira *et al*., 2004, Mihuc and Minshall, 2005; Mellon et al, 2008).

Fire disturbance operates over multiple scales. It can contribute to maintain habitat heterogeneity and biological diversity at the landscape scale, but in other hand, it may lead to the loss of habitat for individuals and small populations at microhabitat level (Pilliod *et al*., 2003).

Mediterranean macroinvertebrate lotic communities are dominated by aquatic insects with a terrestrial phase, so the re-colonization process after a disturbance can be particularly rapid – a few years or less (Verkaik, 2013a) . Also, when disturbance is frequent, communities are usually dominated by taxa exhibiting traits characteristic of pioneer species, such as high dispersal rates, trophic generalism, short generation time and high fecundity (Mihuc and

Minshall, 1995; Arkle et al., 2010, Malison & Paxter, 2010; Vieira et al, 2011; Rugensky & Minshall, 2014).

Several studies that have addressed the impact of wildfires on macroinvertebrate communities, at different time scales (ranging from one year to one decade) showed different recovery times depending on the end-point used to represent “recovery”. Typically, species abundance or density is the first community parameter to recover, which might reach pre-fire levels in less than a year (Roby and Azura, 1995; Minshall *et al*., 1997; Earl and Blinn, 200; Vieira *et al*., 2004). Taxa richness may also have a short-term recovery time, varying between one to four years (Richards and Minshall, 1992; Hall & Lombardozzi, 2008), while community structure and composition may take a longer period to return to the initial state (Minshall *et al*., 2001; Spencer *et al*., 2003; Mihuc and Minshall, 2005; Arkle *et al*., 2010; Malison and Baxter, 2010). Given the alterations of community parameters within the first year after fire impact, this period of time seems critical to describe more comprehensively the changes in biological assemblages associated with post-fire recovery.

The main objective of this study is to document the short-term effects of wildfire (during the first year) on lotic macroinvertebrate communities in Portuguese upland streams. In order to achieve this study aimed to 1) document post-fire disturbance process before and right after the major rainfall events; 2) document the recovery of macroinvertebrate communities in face of these disturbances and early post-disturbance habitat and 3) evaluate the importance of habitat conditions at local, reach and catchment scale in mediating disturbance and facilitating recovery.

3.2 Methods

3.2.1 Study Area

The present study took place in low order upland headwater streams in the North and Central Portugal. Land use in the watershed was dominated by Pine and/or Eucalyptus plantations, and also heathland and scrubland at higher altitudes.

During August 2009, 19 catchments affected by wildfires were selected in North and Central Portugal, representing a gradient between 50 and 100% catchment area affected by fire, and simultaneously considered without any other important sources of impacts related with human activities, such as large urban areas, industry or intensive agriculture (Figure 3.1).

Information related to fire events was provided by the European Forest Fire Information System (EFFIS), and incorporated in a GIS database along with other geographical information including altitude, slope, stream link magnitude, land use and catchment area. After the fire season, characteristics at catchment scale were taken into account to select six references sites in the same geographical area, comparable to fire impact sites with respect to the described variables, but without fire impact for the past 20 years (Table 3.1).

Table 3.1 – Summary of the environmental variables at catchment scale (range) of burnt and reference sites.

Variable (units)	Burnt Sites	Reference Sites
Burnt area (% catchment)	76 ± 20.4	0
Altitude (meters)	480 ± 184.4	590 ± 247.4
Stream Link Magnitude	20 ± 31.1	40 ± 69.0
Catchment area (ha)	338± 551.0	642 ± 822.8
Slope (meters)	132 ± 60.4	81 ± 41.5
Forest area in the catchment (%)	38 ± 35.1	37 ± 26.1
Scrubland area (%)	40 ± 40.0	33 ± 41.5
Agriculture areas (%)	21 ± 27.3	30 ± 24.1

Figure 3.1 – Sampling sites. Burnt sites sampled frequently (black diamonds), burnt sites re-sampled one year after fire (white lozenges) and reference sites (stars).

3.2.2 Sampling Surveys

The first survey was conducted shortly (less than one month) after the fire impact, during September 2009 (n=19 burnt sites), the earliest time it was safe to conduct ecological surveys (Table 3.2). A subset of 10 sampling sites, chosen for frequent survey, was visited in November 2009, March 2010 and May 2010, along with concomitant surveys at reference sites. In late August 2010, one year after the fires, all burnt and reference sites were resurveyed, (n=19 burnt sites; n=6 reference sites).

Macroinvertebrates were collected by kick-sampling in riffle and pools habitats and kick and sweep sampling of submerged woody debris and vegetation, in slow-flowing habitats, using a 500 micrometer mesh pond net.

Sampling effort was divided between riffles (2 minutes sampling), pools (1 minute) and water column substrates (wood, tree roots and/or macrophytes; 1 minute). Samples were preserved separately by habitat type in 70% ethanol. In the laboratory, macroinvertebrates were separated from organic and mineral material in a white tray, under strong light. Macroinvertebrates were identified to species/genus level using a binocular microscope, with the exception of Chironomidae (tribe), Arachnida (family), Annelida (class) and Turbellaria (class).

Table 3.2 – Sampling sites, their UTM coordinates and sampling survey times.

	CODE	UTM	Sep 09	Nov 09	Mar 10	May 10	Aug 10
Burnt sites	BUR	29T 548148 4655973	✔	✔	✔	✔	✔
	ERM	29T 555233 4631109	✔				✔
	GOD	29T 546359 4619275	✔	✔	✔	✔	✔
	COD	29T 545096 4618628	✔				✔
	RBE	29T 599753 4604530	✔	✔	✔	✔	✔
	GON	29T 598722 4601874	✔	✔	✔	✔	✔
	CUN	29T 595837 4599464	✔	✔	✔	✔	✔
	SED	29T 595654 4563341	✔	✔	✔	✔	✔
	PAS	29T 594938 4560900	✔				✔
	AVL	29T 580110 4562340	✔	✔	✔	✔	✔
	GOU	29T 579051 4562435	✔				✔
	VIB	29T 582355 4556692	✔				✔
	RIB	29T 558337 4550520	✔	✔	✔	✔	✔
	CNT	29T 576273 4544985	✔				✔
	DOR	29T 592585 4543137	✔				✔
	ESP	29T 602017 4541644	✔				✔
	SAB	29T 646494 4463689	✔	✔	✔	✔	✔
	RSX	29T 641399 4477046	✔	✔	✔	✔	✔
	SXA	29T 641577 4476299	✔				✔
Reference sites	MIN	29T 549964 4653819		✔	✔	✔	✔
	CBR	29T 601951 4609578		✔	✔	✔	✔
	RPE	29T 603366 4595590		✔	✔	✔	✔
	MAR	29T 589997 4568258		✔	✔	✔	✔
	MAF	29T 591741 4563196		✔	✔	✔	✔
	EST	29T 655557 4454223		✔	✔	✔	✔

Stream habitat characterization, at the reach scale, was made using a modified version of the River Habitat Survey, adapted to Portuguese upland streams (Monaghan and Soares, 2008); observations and measurements were carried out at 10 “spot-check” points, spaced at 20 meter intervals over a 200 meter section of the stream. At each spot-check, bank and channel features such as bank size, substrate, flow type, aquatic vegetation, cover and modifications were registered. Characteristics of the riparian corridor, including shade and vegetation complexity were also recorded (Raven *et al*., 1998). A more detailed complementary description of substrate size was made at macroinvertebrate sampling locations. Water quality parameters including pH, conductivity, dissolved oxygen and temperature were measured, *in situ*, using portable meters and water samples were collected for laboratory analysis of total nitrogen (N), ammonia (NH_4^+), nitrates (NO_3^-), nitrites (NO_2^-), hydrogen cyanide (HCN), total phosphorus (total P), soluble reactive phosphorus (sol P), dissolved silica (Si), chloride (Cl^-) and sulphate (SO_4^{2-}) concentrations.

3.2.3 Data Analysis

Sites physical characteristics were reduced by PCA. Habitat features were divided as descriptors of channel, banks and riparian zone and described by separate ordinations. Ordination scores were used to characterize streams, based on the site’s centroid in ordination space. Management intervention in bank structure represented by reinforced, walled banks was widespread. These bank-modifications were expressed as a ratio between spot-checks with walls and spot-checks without walls; walls adjacent to the wetted channel give a score of 2 and wall set-back from the wetted channel scoring 1 (embankment variable).

Data on water nutrients/dissolved ions were also reduced by PCA, after logarithmic transformation. The scores were used as general summaries of water quality.

The macroinvertebrate community for a given site (reach level) was based on pooled samples (combining riffle, pool and water column samples). Differences in abundance and taxa richness between burnt and reference sites were tested by Mann-Whitney U tests. Differences in terms of community structure and composition between burnt and reference sites were investigated using Analysis of Similarity (ANOSIM). ANOSIM has been widely used for testing spatial and temporal differences between biological assemblages and particularly for detecting environmental impacts (Chapman and Underwood, 1999). This analysis tests the null hypothesis “no differences between the communities” and generates an R value that varies between zero and one, where values closest to zero are given by more similar assemblages. ANOSIM was undertaken on logarithmic transformed abundance data, using Bray Curtis dissimilarity scores. Significance of ANOSIM was tested using Monte Carlo permutation test with 999 permutations. Complementary to ANOSIM, Non-metric multidimensional scaling (NMDS) was used to represent the similarities between macroinvertebrate community structures between sampling sites in each sampling season. Similarity Percentages (SIMPER) analysis was used to determine which taxa contributed the most to differences between burnt and reference sites.

To determine which variables influenced the fire impact and recovery of macroinvertebrate communities, the relationship between assemblages of burnt sites and environmental variables were investigated using Redundancy Analysis (RDA). Environmental variables were standardized and biological data were transformed by Hellinger transformation. This latter transformation allows the application of Euclidean-based ordinations, such as RDA, by eliminating the double-zeros problem and making the analysis suitable for biological data sets (Legendre and Gallagher, 2001). Forward selection was used in RDA to select the subset of variables that provided the highest explanatory model. The significance of each variable was calculated by 999 permutations in Monte Carlo test and variables with $p<0.05$ were included in the constrained ordination model. In order to better interpret the influence of environmental variables on macroinvertebrate communities, a “Locally weighted scatter plot smooth” –

LOESS, was plotted, illustrating the fitting of taxa richness and abundance in ordination space.

All the analysis was performed on R software, except RDA, performed on CANOCO 4.5 software.

3.3 Results

3.3.1 Physical habitat

The first two ordination axes of channel characteristics explained 44.27% of the total variability of physical habitat. The first axis (Channel-1) represented 25.40% of the variation and described a transition between fast-flowing streams with larger substrate, low embeddedness and in-stream vegetation dominated by moss to slower streams with smaller substrate and high embeddedness, where in-stream vascular plants were more common and an increased tendency for submerged terrestrial vegetation was observed (Table 3.3). The second axis, Channel-2 (18.87%) described a gradient in width and depth, ranging from deeper and wide streams, with more in-stream cover to shallow, narrow streams with less cover.

The primary axis of bank features (Bank-1) explained 29.01% of total variability describing a trend from streams with low banks, smaller material with more eroding undercut banks to streams with high banks and larger material, less prone to erosion. Bank-2 (17.06%) ranged from sites with narrow banks to streams with wider banks and more deposition associated with sidebars and middle channel bars.

Primary variation in riparian vegetation (Riparian-1) captured 27.56% of the global variation and describes a decrease in the complexity of the riparian vegetation structure, from complex to bare ground, closer to the stream (until 1 meter), along with the decrease of tree shadow and an increase of herbaceous shadow. The second axis (Riparian-2) explained 19.60% of the total variation and described an increase in vegetation complexity from 1 to 5 meters distance

from the waters edge (a gradient from grasslands/pastures to eucalyptus/pine plantations and broadleaf woodland) and a decrease in the complexity of riparian vegetation.

The variation of water quality was largely explained in the primary axis (41.08%) by the increase of silica and chloride along with the increases of nitrates, total Nitrogen, sulphates, phosphates, Silica and Chloride (Water-1).

Table 3.3 - Summary of principal component axes based on PCA of habitat features (channel, bank, riparian zone and water quality). Values indicate the weightings for respective variables

Channel-1	Channel-2	Bank-1	Bank-2	Riparian-1	Riparian-2	Water-1
Vascular Plants **- 1.846**	In-stream cover **0.778**	Undercuts **-1.544**	Sidebars **2.009**	Left 1meter Complexity **- 2.208**	Left face complexity **- 1.872**	Phosphates **0.087**
Submerged terrestrial vegetation **- 1.747**	Width **2.568**	Left height **1.626**	Bank width **2.253**	Right 1meter complexity **- 2.093**	Right face complexity **- 1.775**	Sulphates **0.506**
Embeddedness **- 1.506**	Depth **2.601**	Right height **1.819**		Tree shade **- 2.012**	Left 5meters complexity **1.634**	Nitrogen **0.552**
Flow **1.693**		Left material **2.303**		Herbaceous shade **1.265**	Right 5meters complexity **2.015**	Dissolved Silica **0.572**
Moss **1.759**		Right material **2.471**				Nitrates **0.643**
Substrate **2.497**						Chloride 0.862

Biological data

Over the five sampling periods, 259 taxa were identified, mostly belonging to the Insecta class (92%). In both burnt and reference sites, Diptera was the most abundant order, representing 45.57% and 30.36% of the total of individuals, respectively. For burnt sites, Diptera were followed by Coleoptera (13.45%) > Plecoptera (12.95%) > Ephemeroptera (10.21%) > Trichoptera (9.98%) > non-insect taxa (3.82%) > Odonata (3.00%) > Heteroptera (0.56%) and Megaloptera (0.45%). Reference sites showed a higher percentage of Ephemeroptera and Plecoptera (19.58% and 18.64%) followed by Coleoptera (11.70%) > Trichoptera (11.28%) > non-insect taxa (5.20%) > Odonata (2.13%) > Heteroptera (1.09%) and Megaloptera (0.03%).

The annual variation of abundance and taxa richness for burnt and reference sites are showed in figure 3.2 (A and B, respectively). Abundance was significant lower in March, May and August, while the differences for taxa richness between burnt and non-impacted sites were significant for all sampling periods (Table 3.4).

When data from summer 2009 and summer 2010 were compared, for burnt sites only, abundance values were significantly lower one year post-fire (Mann-Whitney U=140.00; p=0.006) while taxa richness recovered to post-fire values, demonstrating no significant difference (Mann-Whitney U=88.00; p=0.246).

Table 3.4 – Mann-Whitney test results from the comparison of abundance and taxa richness between burnt and reference sites, per sampling season.

Measure	Season	Mann-Whitney U	p-value
Abundance	November	16.00	0.147
	March	2.00	0.002
	May	0.00	0.000
	August	1.00	0.000
Taxa Richness	November	8.50	0.016
	March	3.00	0.003
	May	4.00	0.005
	August	5.00	0.000

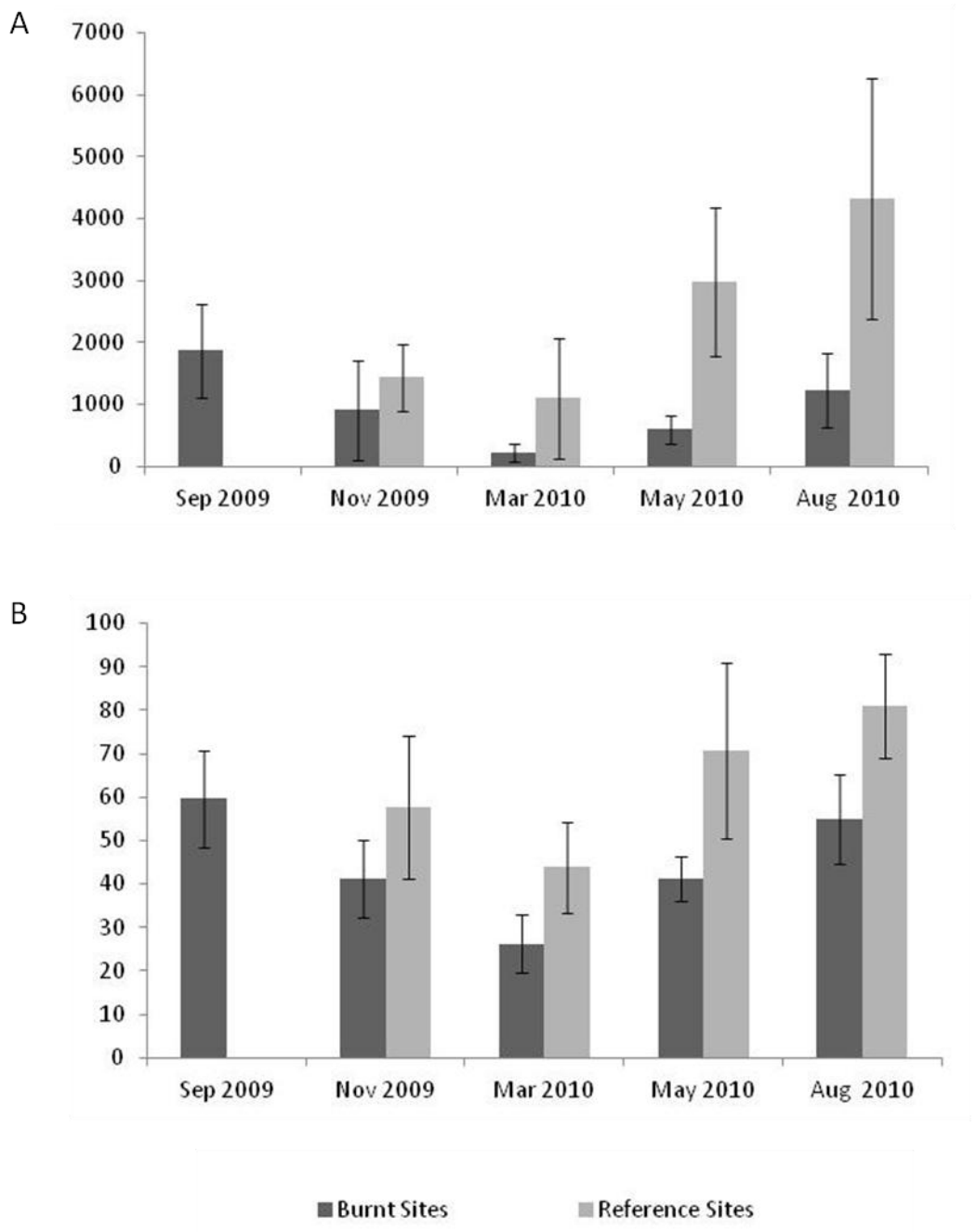

Figure 3.2 – Abundance (A) and taxa richness (B) per sampling periods (mean value ± standard deviation) of burnt (dark grey) and reference (light grey) sites.

Analysis of Similarity (ANOSIM) showed that community structure on reference sites and burnt sites was significantly different, in all sampling periods (figure 3.3). The differences increased until May, then decreased again in

August. These results are consistent with the ones obtained by the NMDS ordination analysis (figure 3.4): the differences between burnt and reference sites increase in spring sampling periods (March and May) and are less evident in November and August.

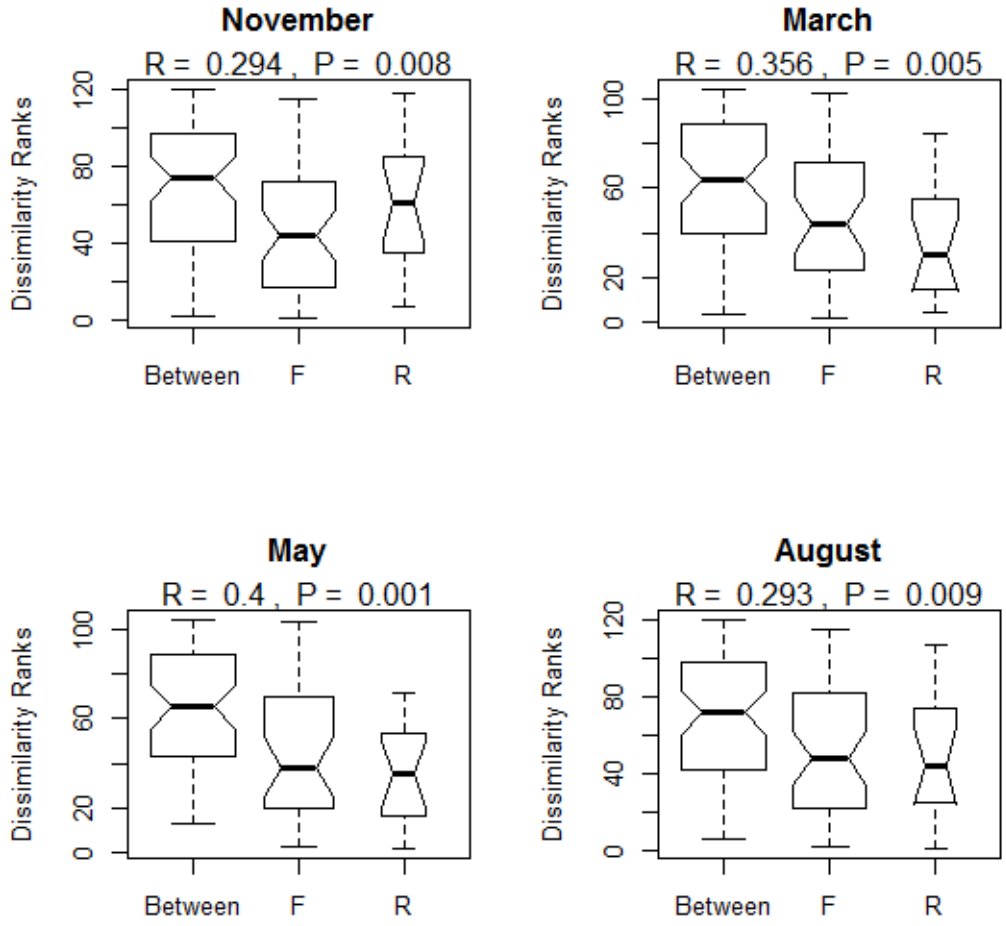

Figure 3.3 - Boxplots with Analysis of Similarity (ANOSIM) results per sampling season. “Between” represent dissimilarity ranks between burnt and reference sites; (F) dissimilarity within group of burnt samples; (R) for dissimilarity within reference sites group.

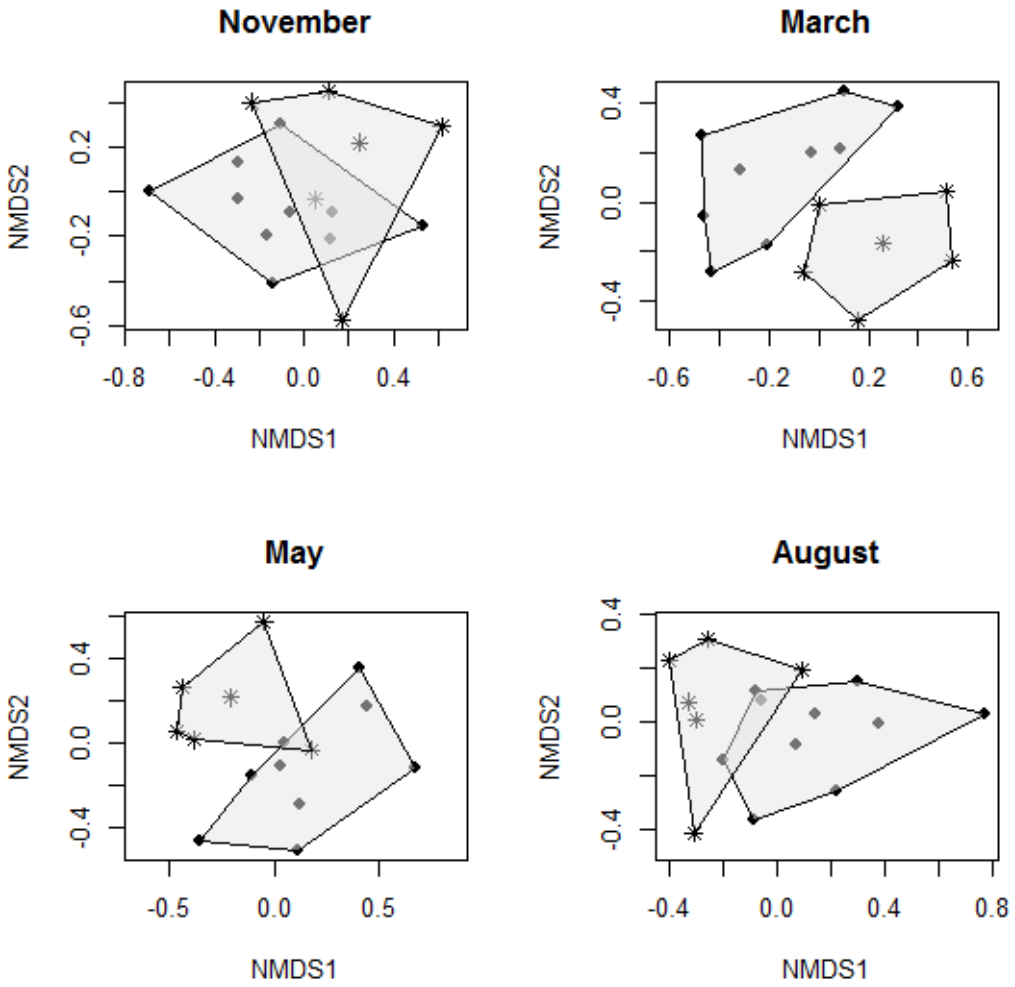

Figure 3.4 –Two-dimensions NMDS plots of the macroinvertebrate communities based on Bray-Curtis resemblance matrix, per sampling season. Diamonds in the plots space represent burnt sites and stars represent reference sites.

In November, taxa contributing the most for the recorded difference were Capnioneura sp. stonefly, several genus of the Limnephilidae family and black fly *Simulium* sp., with higher relative abundances at reference sites. In March and May stoneflies *(Leuctra* sp. and *Protonemura* sp.) and mayflies (*Ecdyonurus* sp. and *Habrophlebia* sp.) were the most influencial taxa in the ANOSIM analysis, being present in reference sites with higher relative abundances. In August, differences where due to *Habrophlebia* sp., the water beetle *Oulimnius* sp. and caddis fly *Hydropsyche* sp., more represented also in reference sites (Table 3.5).

Table 3.5 – Mean abundance (MAb, log transformed data) of taxa contributing up to 10% of Bray–Curtis similarity (similarity percentages analysis) between burnt and reference sites samples from sites

Taxon	MAb. burnt sites	MAb. ref sites	% contribution
November 2009			
Capnioneura sp.	1.39	2.94	2.18
Potamophylax sp.	0.70	2.68	2.16
Simulim sp.	3.36	3.45	2.00
Chaetoptheryx sp.	0.51	2.44	1.96
Hydropshyche siltalai	0.60	2.63	1.94
March 2010			
Leuctra sp.	0.34	3.29	3.74
Protonemura intricata	1.49	3.24	3.02
Simulium sp.	2.09	3.26	2.92
Ecdyonurus sp.	1.12	2.17	2.32
May 2010			
Leuctra sp.	1.83	5.52	2.70
Habrophlebia sp.	0.75	3.53	2.42
Protonemura intricata	2.42	4.32	2.00
Oulimnius sp. (larvae)	0.23	2.82	1.86
Ecdyonurus sp.	0.89	2.80	1.66
August 2010			
Habrophlebia sp.	3.17	5.44	1.53
Oulimnius sp. (larvae)	1.40	3.00	1.49
Hydropshyche tibialis	1.51	3.00	1.44
Turbellaria	0.49	2.54	1.43
Sericostoma sp.	1.55	2.87	1.43
Calopteryx virgo	0.96	3.07	1.41
Plectrocnemia sp.	0.25	2.50	1.37

3.3.2 Relationship between biological data and environmental data

According to the Redundancy Analysis, 11 variables were correlated with macroinvertebrate assemblages from burnt sites, explaining 36.7% of the total variability of biological data (Table 3.6). Monte Carlo permutation test performed for all canonical axes showed the statistical significance of the model (F=2.852; p=0.001). The first RDA axis, representing 25.1% of species-environment variance was positively related to stream link magnitude, burnt catchment area, bank-2, channel-2, riparian-1 and stream embankment and negatively associated with altitude, slope and riparian-2. The second axis (21.8% of species-environmental variance) was positively related with channel-1 and showed a negative correlation with temperature, the only variable at the local scale that was incorporated in the redundancy model (Figure 3.5).

Table 3.6 – Conditional effect (λ) and significance of environmental variables included in the Redundancy Analysis (RDA) model. Variables are shown by the order of importance.

Variables	Conditional effect (λ)	F	p-value
Temperature	0.07	5.004	0.0010
Stream link magnitude	0.07	4.558	0.0010
Altitude	0.04	3.580	0.0010
Channel-1	0.04	2.832	0.0010
Riparian-2	0.02	2.056	0.0020
Embankment	0.03	1.962	0.0050
Bank-2	0.02	1.643	0.0250
Burnt catchment area	0.02	1.575	0.0350
Slope	0.02	1.540	0.0420
Channel-2	0.02	1.740	0.0200
Riparian-1	0.02	1.129	0.0180

Looking at taxa richness (figure 3.5A) and abundance (figure 3.5B) gradients in the ordination space revealed higher values of water temperatures were associated with higher abundance and taxa richness. At the catchment level, stream size and percentage of catchment burnt were associated with richness and abundance of macroinvertebrates. Bigger streams were related to the highest taxa richness and abundance; the percentage of burnt area was negatively related to both parameters.

At the reach scale, impacted sites with lower abundance and taxa richness, were associated with deeper and wider channels, more in-stream cover, a higher percentages of bank side bars and less complex riparian vegetation and less shade. Human intervention in stream channels, here represented by the variable embankment, clearly had a negative impact on both abundance and taxa richness of burnt streams.

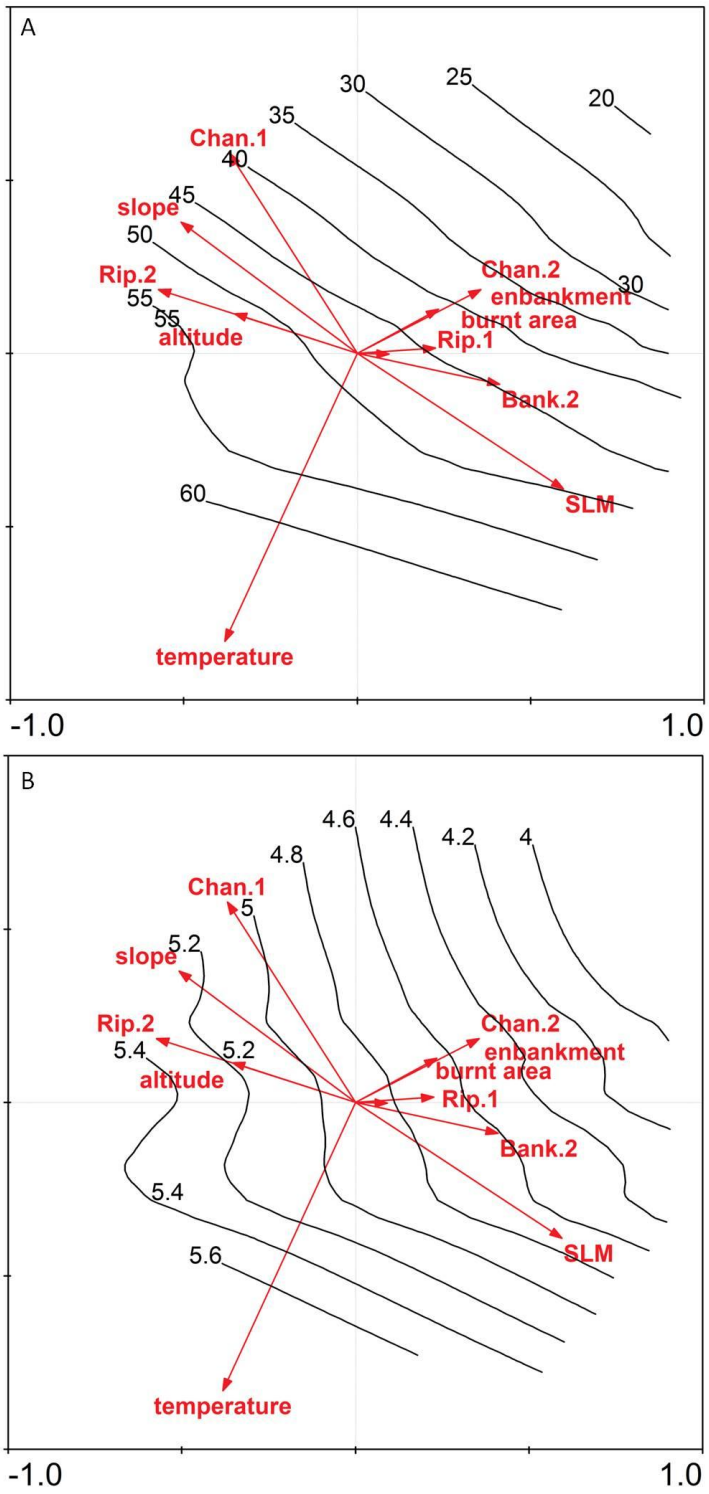

Figure 3.5 – Biplots based on Redundancy Analysis (RDA) representing the correlation between biological data (Hellinger transformed) and significant environmental variables: temperature, stream link magnitude (SLM), altitude, channel features (Chan.1 and Chan.2), riparian vegetation (Rip.1 and Rip.2), bank characteristics (Bank.2), embankment, catchment area burnt and slope. Locally weighted scatter plot smoothing lines are also represented, fitting taxa richness (plot A) and log transformed taxa abundance (plot B).

3.4 Discussion

3.4.1 Fire impact on taxa richness and abundance

The strongest effects of wildfire on lotic communities are often associated with the consequences of post-fire precipitation (Rinne, 1996; Bisson *et al*., 2003; Verkaik *et al.*, 2014). Direct effects of fire are often negligible (except in cases of heating of small water volumes or exposure to dense smoke), so it seems reasonable to consider that immediate post-fire and pre-fire macroinvertebrate assemblages were probably very similar and collections made shortly after fire events could be used as references in these type of studies (Minshall, 2003), which was confirmed by this study. Nevertheless, we decided to focus our comparisons with carefully chosen reference sites, without recorded fire events in the past 20 years, to reinforce data interpretation.

Taxa richness and abundance at burnt sites were reduced by fire, being significantly lower for all sampling periods except for November, when no differences in abundance were evident. Despite some important rain events in November, the higher precipitation rates from 2009/2010 took place between December and March, which may explain the greater differences found in spring sampling.

3.4.2 Fire impact on community composition and structure

Community composition between burnt and reference sites differed on all sampling occasions. NMDS showed some overlap of the two groups of communities in November, which corroborates with the lowest value of R in the ANOSIM test (R=0.294; p=0.008). Both analyses indicated that the greatest differences were found in March and May but a slight recovery seemed to have occured towards summer, which can also be explained by the annual variation of precipitation during the survey.

Recovery in terms of community composition and structure often takes longer than in taxa richness and abundance. Reviewing the impact of wildfires

on benthic macroinvertebrate in Mediterranean rivers Verkaik *et al.*, (2013), concluded that both richness and abundance recovered to values close from reference sites within three months, but significant differences in community composition remained. Similar results were obtained by other authors for different geographical areas (Minshall *et al.*, 1997; Tronstad *et al*., 2010).

SIMPER analysis revealed that most differences between burnt and reference sites were related to the lower percentage of Plecoptera Ephemeroptera, and Trichoptera taxa in burnt sites, probably reflecting the sensitivity of those taxa to reduced water quality and habitat degradation. Several genera from Nemouridae, Capniidae and Leuctridae can behave mainly as detritivores-herbivorus in southern latitudes (Azzouz and Sanchez-Ortega, 2000), so the sensitivity of these taxa to fire impact may be connected with a decrease of food availability (Mihuc and Minshall, 1995). *Ecdyonurus* sp. was the Ephemeroptera that mostly contributed to the differences recorded in March and May, which can be explained by the lesser mobility of flattened form species, which makes them more susceptible to sedimentation (Minshall, 2003). On a study of Trichopera and several types of environmental stress, Kalaninová *et al.* (2014) found lower taxa richness and a lower percentage of specialist-feeders in communities impacted by fire, which is consistent with our data.

3.4.3 Environmental variables affecting fire impact

The only variable at the local scale that was select by the RDA model was water temperature, which reflects the natural seasonal variation in environmental conditions and macroinvertebrate communities (Soulsby *et al*., 2001). Portuguese streams, with high species diversity, are more likely to show variations in life cycles, and therefore higher seasonal differences (Feio *et al.,* 2006).

As discussed in chapter two, the size of the stream has an important influence on the biological response to wildfire with this study revealing a greater impact in small streams. In small rivers, a greater proportion of the

adjacent catchment is likely to be burned and the ratio between riparian vegetation and water volume is high (Minshall *et al.*, 1997; Melon *et al*., 2008). On the other hand steeper slopes and high altitudes seemed to promote a faster recovery of taxa richness and abundance of macroinvertebrates, an apparent contradiction, since upland streams are usually represent a lower stream order. In these upland Portuguese streams small, high altitudes streams with steep valleys often helps to preserve riparian vegetation from burning by escaping the fire. North-American studies have demonstrated that, for mountain areas, fire frequency and severity in riparian corridors can be lower than those in the associated upland forests (Dwire and Kauffman, 2003; Kozbiar and McBride, 2006). Riparian vegetation is highly influential on stream ecology, since it regulates the movement of species, as well as water and nutrients, contributing also to bank stability and habitat structure (Pettit and Naiman, 2007).

Descriptors of channel and bank variables in our analysis were congruent with the impact of increased erosion and post-fire channel alteration described by several authors (Benda et al., 2003; Dunham et al., 2007; Bendix and Cowell, 2011). Negative impacts on macroinvertebrate communities were related to an increased frequency of side-bars and an increased ratio of pool-riffle habitats (burnt streams showed a high percentage of standing water sites). This reorganization of stream channels by large amounts of sediment input and wood debris has been associated with direct mortality not only on macroinvertebrates (Minshall, 2003) but also amphibians (Pilliod *et al.*, 2003), and fish communities (Rieman *et al.*, 1997; Burton 2005).

Artificial embankments interfere with the natural flow and sediment transport of rivers (Cortes *et al*., 2002). The widespread occurrence of channelization and walls reinforcing in the river systems of central and north Portugal (Monaghan and Soares, 2008), may exacerbate the impact of wildfire on the biological communities Portuguese rivers.

3.5 Conclusion

Significant differences were found in all ecological parameters measured (taxa richness, abundance, community structure) between burnt sites and reference sites. The ecological impact was evident after the first major rain events in autumn and, despite some signs of recovery towards summer, differences were still recorded one year after the fire.

Both catchment scale and reach scale environmental characteristics seems to influence the intensity of macroinvertebrate communities to fire disturbance. At catchment scale, river size, altitude, slope and the extend of burnt area were related to biological data; at reach scale, bank and channel features, riparian vegetation complexity and the degree of stream embankment were considered to influence macroinvertebrate assemblages.

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4 The impact of wildfire on functional composition and structure of macroinvertebrate communities

4.1 Introduction

Over the last two decades, trait-based analytical approaches have been widely used by ecologists (Menezes *et al*., 2010). It is considered to be a powerful tool for monitoring and management of stream ecosystems because it is grounded in functional adaptations and is therefore informative about natural and human disturbance (Townsend and Hildrew, 1994; Dolédec *et al.,* 1999). Groups with similar biological and ecological traits are expected to respond consistently along specific environmental gradients, so by using taxa traits instead of taxonomic identities, researchers can overcome the difficulties associated with predicting taxa composition in lotic systems, taxonomic uncertainty and improve cost-efficiency (Poff *et al.,* 2006). By definition, a functional trait is “any trait which impacts individual fitness indirectly via its effects on growth, reproduction and survival” (Violle *et al.*, 2007).

Mediterranean streams are physically, chemically and biologically shaped by a series of sequential and probabilistic events of flooding and drying during the annual cycle (Gasith and Resh, 1999) and, therefore, macroinvertebrate lotic communities exhibit a set of traits conferring resistance (e.g., reproduction through terrestrial clutches, diapauses or specialized respiration techniques) and resilience (e.g. small body size, frequent reproduction cycles and aerial active dispersal, favouring rapid colonization) to thrive in Mediterranean streams (Bonada *et al.,* 2007a). These characteristics can be particularly important to the response to fire disturbance by determining the degree of vulnerability of Mediterranean macroinvertebrate communities to fire impact and their ability to recovery, thereafter.

Previous research has revealed the importance of traits on fire impact in river ecosystems, primarily in relation to changes to food webs dynamics and feedings groups (e.g., Mihuc and Minshall, 1995 and 2005) but also in terms of colonization capacity and dispersal (Viera *et al.*, 2004), suggesting the value of a trait-based analysis to help understand the processes of disturbance and recovery.

Trait-based approaches for Portuguese macroinvertebrate communities have been applied to various issues such as bioassessment (Cortes *et al*., 2013; Hughes *et al.*, 2010; Varandas and Cortes, 2010), extreme climatic events (Feio *et al.,* 2010) and natural ecological gradients (Pinto *et al*., 2019). Although wildfires are a common disturbance whose effects in Mediterranean lotic systems is still little known, a comprehensive study of its effects at an ecological functional level has not previously been documented.

In the present work, our goal was to understand the influence of fire disturbance on the functional organization of macroinvertebrate communities. In order to do that, our specific research objectives were to determine: 1) how does fire impact influence functional diversity; 2) what is the influence of fire disturbance on functional structure; and, 3) how do environmental variables influence the trait community structure of post-fire recovery.

4.2 Methods

4.2.1 Study Area

The present study took place in low order upland headwater streams in the North and Central Portugal. Land use was dominated mainly by Pine spp. and/or Eucalyptus spp. plantations, but also heathland and scrubland at higher altitudes.

During August 2009, 19 catchments affect by wildfires were selected in North and Central Portugal, representing a gradient between 50 and 100% of the catchment area burned. All study sites were free from any other major source of impact related to human activities, such as large urban areas, industry or intensive agriculture (Figure 4.1).

Information related to fire events was provided by the European Forest Fire Information System (EFFIS), and incorporated in a GIS database along with other geographical information such as altitude, slope, stream link magnitude, land use and catchment area. After the fire season, characteristics

at the catchment scale were taken into account and used to select six references sites in the same geographical area, comparable to fire impact sites with respect to the described variables, but without fire impact for the past 20 years.

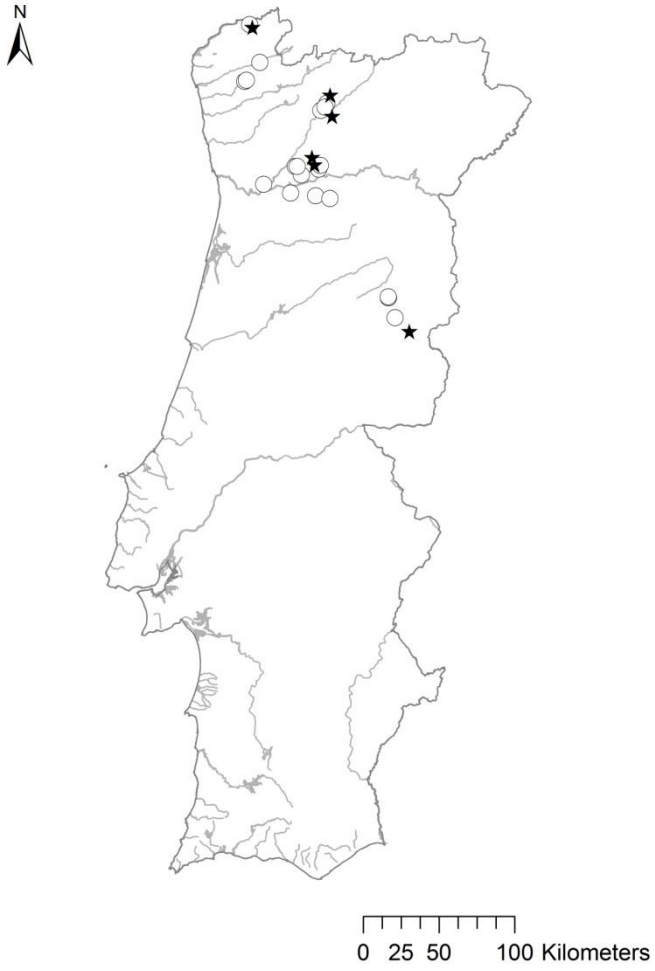

Figure 4.1 – Sampling sites (burnt sites = white dots; reference sites = stars).

4.2.2 Sampling Surveys

Four surveys were conducted within one year after fire impact, in November 2009, March 2010 and May 2010 (burnt sites=10 and reference sites=6) and August 2010 (burnt sites=19 and reference sites=6). The

frequency of the surveys was determined by the prior knowledge of the rapid recovery of the communities, as described in chapter 2.

Macroinvertebrates were collected by kick-sampling in riffles and kick and sweep sampling in pool habitats and from submerged woody debris and submerged vegetation using a 500 micrometer mesh pond net. Sampling effort was divided between riffles (2 minutes sampling), pools (1 minute) and water column substrates (wood, tree roots and/or macrophytes; 1 minute). Samples were preserved separately by habitat type in 70% ethanol. In the laboratory macroinvertebrates were sorted from organic and mineral material in a white tray, under strong light. Macroinvertebrates were identified to genus level (the taxonomic level of the most common trait databases), with the exception of Chironomidae (tribe), Arachnida (family), Annelida (class) and Turbellaria (class).

Stream habitat characterization, at the reach scale, was made by a modified version of River Habitat Survey, adapted to Portuguese up land streams (Monaghan and Soares, 2008); observations and measurements were carried out at 10 “spot-check” points, spaced at 20 meter intervals over a 200 meter length section of the stream. At each spot-check bank and channel features such as bank height, substrate size, flow type, aquatic vegetation structure, cover and human modifications were registered. Characteristics of the riparian corridor, including shade and vegetation complexity were also recorded (Raven *et al*., 1998). A more detailed complementary description of macroinvertebrate habitat (in terms of substrate size) was made at macroinvertebrate sampling locations. Water quality parameters including pH, conductivity and temperature were measured, *in situ*, using portable meters and water samples were collected for laboratory analysis of nitrogen (N), ammonia (NH_4^+), nitrates (NO_3^-), nitrites (NO_2^-), hydrogen cyanide (HCN), total phosphorus (total P), soluble reactive phosphorus (sol P), dissolved silica (Si), chloride (Cl^-) and sulphate (SO_4^{2-}) concentrations.

Bank, channel and riparian features and parameters of water quality, were reduced to general gradients by Principal Component Analysis. A

description of environmental variables as they appear in results is presented in Table 4.1.

Table 4.1 – List of environmental variables used in this study. See Table 3.2 for further details on gradients described and variables description.

Variable	Description
Conductivity	Conductivity measured at macroinvertebrates sampling point (S/m)
Temperature	Water temperature measured at macroinvertebrates sampling point (°C)
pH	pH measured at macroinvertebrates sampling point
Burnt area	Percentage of burnt catchment
SLM	Stream Link Magnitude
Altitude	Altitude of sampling point (meters)
Slope	Slope of sampling point (metes)
Forest	Percentage of catchment occupied with forest
Bank-1	Gradient describing the transition from lower banks with small size material to higher banks with large size material
Bank-2	Gradient describing the increase of bank width and number of side bars
Channel-1	Gradient describing the transition from channels with slow current, smaller substrate size and in-stream vascular plants to channels with rapid current, larger substrate size and in-stream moss
Channel-2	Gradient describing the transition from narrow and shallow channels to wider and deeper channels
Riparian-1	Gradient describing the decrease of complexity of riparian vegetation (1 meter from channel) and the decrease of shadow
Riparian-2	Gradient describing de decrease of complexity of channel face vegetation and the increase of complexity of riparian vegetation (5 meters from channel)
Water-1	Gradient describing the increase of nutrients
Embankment	Scale of increasing of channel embankment or channelization

4.2.3 Community traits characterization

A specific database was constructed for the purpose of this work, describing identified taxa in terms of 19 traits divided into 103 modalities (Table 4.2). The chosen traits were adapted from Usseglio-Polatera *et al*., 2000, and were compiled by Tachet *et al.* (2000) and reflect several biological, physiological and ecological features of macroinvertebrates related with their life-cycle, feeding habits, reproductive strategies or habitat requirements, etc.

Following Chevenet *et al.* (1994), a fuzzy coding approach was used to express the affinity of each taxon for a given modality. In this system, for a given trait, a score ranging from zero (meaning “no affinity”) to 5 (high affinity) was assigned to each category. The main source of information was Tachet *et al.* 2000, but information gaps were filled using “freshwaterecology.info” database (Schmidt-Kloibe and Hering, 2012). For taxa with no trait information available, coding was done by calculating the mean value for taxa within the same taxonomic level.

Table 4.2 – Biological and ecological macroinvertebrate traits and respective modalities (adapted from Usseglio-Polatera *et al*., 2000).

Trait	Modality	Trait	Modality
Maximum size	• < 2,5 mm • 2,5 - 5,0 mm • 5 - 10 mm • 10 - 20 • 20 - 40 • 40 - 80	Thermal	• cold (<15°C) • warm (>15°C) • eurytherme
Life cycle	• <=1 year • > 1 year	pH	• <4 • 4-4,5 • 4,5-5 • 5-5,5 • 5,5-6 • >6
Generations	• <1 • 1 • >1	Trophic degree	• oligotrophic • mesotrophic • eutrophic
Aquatic stage	• eggs • larve • nymph • adult	Saprobic value	• xenosaprobic • oligosaprobic • β mesoprobic • α mesoprobic • polysaprobic
Reproduction	• ovoviparity • isolated free eggs • isolated fixed eggs • fixed clutches, cimented • free clutches • endophytic clutches • terrestrial clutches • asexual	Longitudinal distribution	• crenon • epirhithron • metarhithron • hyporhithron • epipotamon • metapotamon • estuary • off river
Dispersal	• aquatic passive • aquatic active • aerial passive • aerial active	Transversal distribution	• river channel • bank, secundary channels • ponds, pools, meanders • marshes, bogs • temporary waters • lakes
Resistance forms	• eggs, shells, gemmules, statoblasts • cocoons • diapause or quiescence • none		
Food	• fine sediment • debris<1mm • plant debris>1mm • microphytes • macrophytes • dead animals • microinvertebrates • macroinvertebrates • vertebrates	Microhabitat	• bedrock to pebble • gravel • sand • silt • macrophytes, algae • microphytes • branches, roots • litter • clay
Feeding	• fine seds • shredder • scraper/grazer • filterer • piecer • predator • parasite	Locomotion	• flight • surface swimmer • open water swimmer • crawling • burrowing (epibenthic) • endobenthic (subsurface) • fixed, temporary • fixed perminant
Respiration	• tegument • gills • plastron • siphon	Current Preferences	• standing waters • slow (<25 cm/s) • medium (25-50 cm/s) • rapid (>50cm/s)

4.2.4. Data Analysis

Functional diversity

The functional diversity (FD) was calculated, for each trait, on the basis of the Rao's index of diversity (Rao, 1982). This index expresses the dissimilarity in trait space among all possible pairs of taxa, weighted by the product of taxa's relative abundance and describes the variation of taxa trait composition within the community (de Bello *et al.*, 2009). First, the dissimilarity between taxa was computed using a taxa by trait matrix, where fuzzy categories were transformed to represent relative frequencies within each trait. Second, trait dissimilarities between sites were calculated crossing taxa by traits matrix with taxa relative abundance per site matrix. Taxa abundance was previously log-transformed in order to decrease the importance of dominant taxa traits in the calculation of functional diversity (de Bello *et al.*, 2007). Differences between functional diversity on burnt sites and references sites were tested by Mann-Whitney U test. The statistical analysis was performed on IBM SPSS Statistics 20 software.

Trait frequencies

The relative frequencies of each trait modality per site were calculated, weighted by taxa's relative abundance. Differences in frequencies between burnt and reference sites were tested by Mann-Whitney U test (IBM SPSS Statistics 20 software).

Relationship between trait composition and environment

In order to assess the link between trait composition and environmental variables, a RLQ analysis was used in combination with a fourth-corner analysis. These, and the following described analyses, were carried out using the ADE4 package of R 3.0.2 software.

RLQ analysis is a multivariate technique that calculates the double inertia between two arrays (R representing environmental variables and Q representing taxa traits), with a link expressed by a contingency table (L

representing taxa abundance), resulting in an ordination whose scores reflect the relationship among taxa traits and environmental variables in a single step (Dolédec *et al.*, 1996).

Prior to RLQ analysis, three separate ordinations of the R, L and Q tables were performed. First, the taxa abundance table, containing log-transformed taxa abundance per site (L), was analyzed by correspondence analysis (CA). The second procedure was to investigate the relationship between sites and environmental variables (R table). Several catchment and site variables were used (Table 4.1), as well as descriptors for channel, bank and riparian vegetation. These data were standardized and a PCA was conducted for RLQ, using weights obtained with the correspondence analysis (CA) of taxa, thereby linking R to L table. The third step consisted in analyzing the Q table of fuzzy coded trait categories with a fuzzy correspondence analysis (FCA), also weighting with the results of CA taxa analysis. RLQ combined the three separate ordinations and maximized the co-variation between environmental variables and traits. The site scores in the R table constrained the site scores in the L table and the taxa scores in the Q table constrained the taxa scores in L table. Within these constraints, axes that maximize covariance between the R and Q tables are selected (Dolédec *et al.* 1996). The global significance of RLQ analysis was calculated through a Monte-Carlo permutation test, with 999 permutations.

Fourth-corner analysis, first proposed by Legendre *et al.* (1997), investigates individual trait-environment correlation through permutation procedures, testing one trait and one environmental variable at a time. In the present work, the forth-corner analysis was used as a complement to RLQ analysis, testing the significance of the correlation between environmental variables and taxa traits with RLQ axes (a detailed description of this combined methodology can be found in Dray *et al*., 2014). Fourth-corner analysis was conducted based on 999 permutations and correlations were considered significant when the adjusted p-value (adjustment by “false discovery rate” method) was lower than 0.05.

4.3 Results

4.3.1 Impact of fire on Functional Diversity (FD)

Results from the variation of the Rao's index of functional diversity, on each sampling period, are present in figure 4.2.

Significant differences were apparent for thermal preferences, in March, when burnt sites showed higher diversity than references sites. No significant differences were found for the spring sampling periods, for any traits. In August, one year after fire impact, differences were apparent for number of generations per year, reproduction, dispersal, resistance forms and current preferences, all of which were significantly higher for reference sites (table 4.3).

Table 4.3 – Mann-Whitney test results for the significant differences between functional diversity for respective traits between burnt (Fire) and reference (Ref) sites, for respective sampling season.

Sampling period	Trait	Mann-Whitney U	p-value	Trend
March	Thermal	10.00	0.050	Fire > Ref
August	Generations	25.00	0.043	Ref > Fire
	Reproduction	18.00	0.011	Ref > Fire
	Dispersal	22.00	0.025	Ref > Fire
	Resistance form	20.00	0.017	Ref > Fire
	Current preferences	20.00	0.017	Ref > Fire

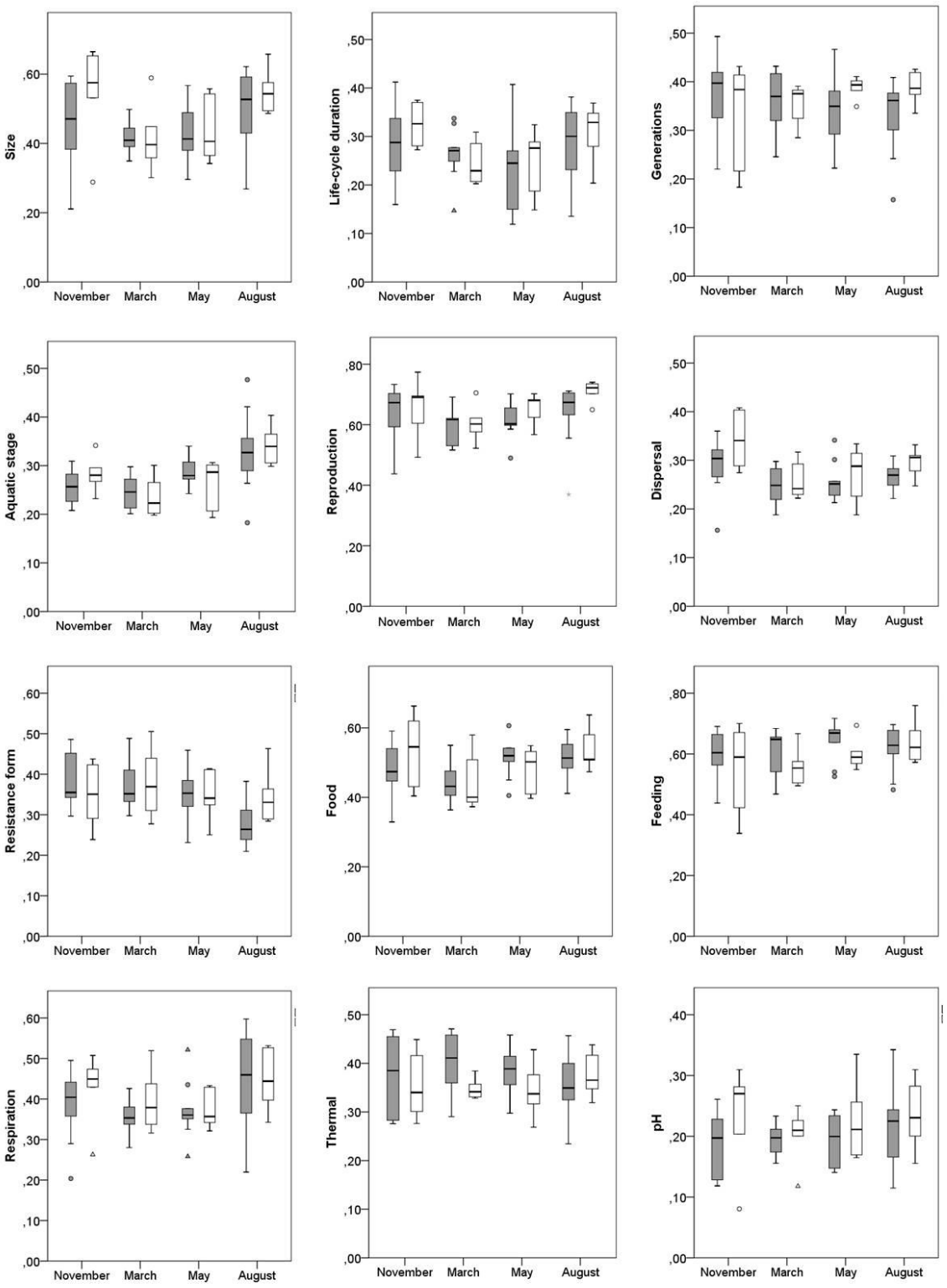

Figure 4.2 – Boxplots representing variation of functional diversity for analyzed trait for respective sampling period. Burnt sites are represented by the grey bars and reference sites are represented by the white bars *(see continuation in the next page)*.

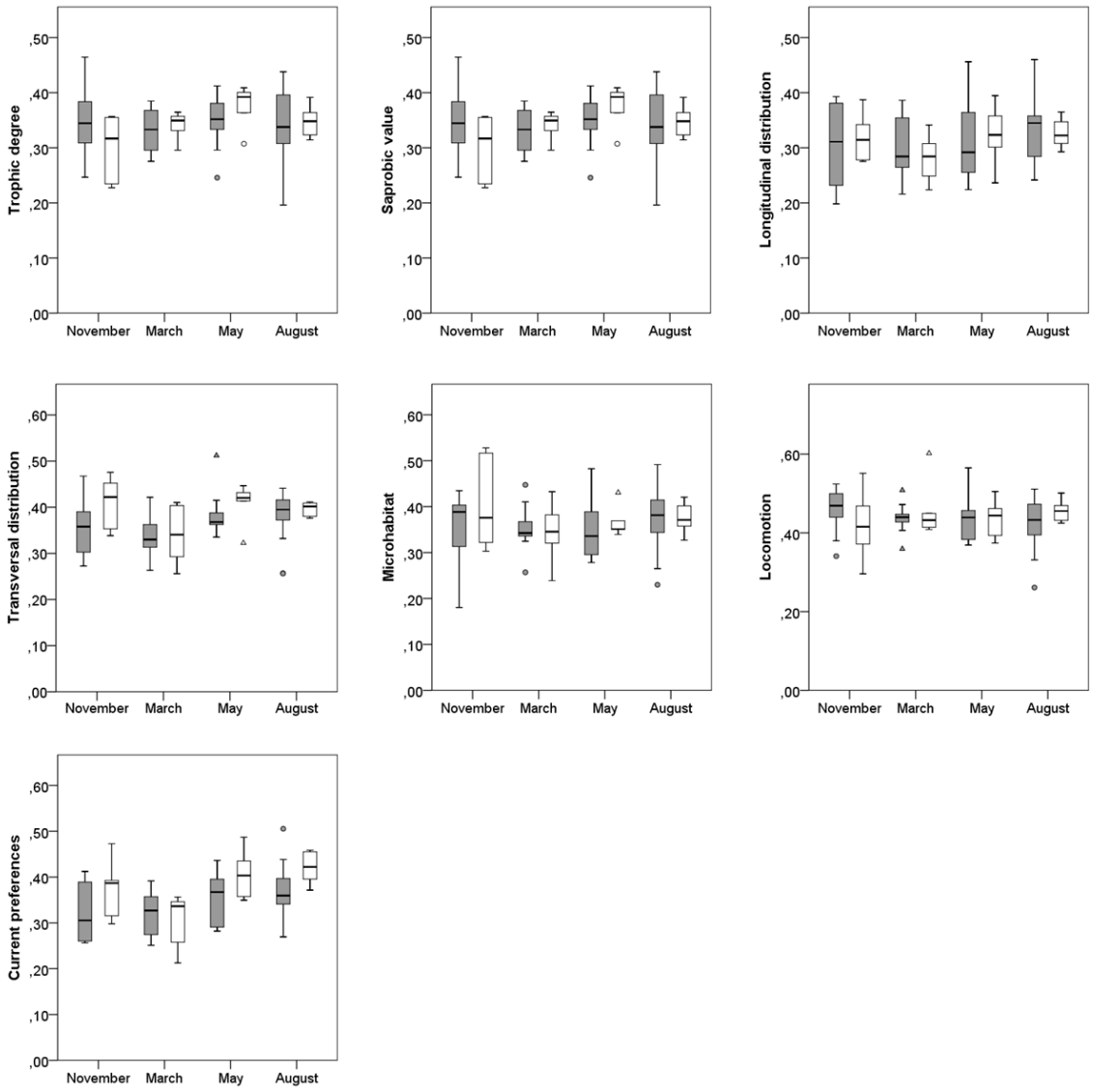

Figure 4.2 (cont.) – Boxplots representing the variation of functional diversity for analyzed traits for respective sampling period. Burnt sites are represented by the grey bars and reference sites are represented by the white bars.

4.3.2 Impact of fire on functional structure

When relative frequencies of each trait modality were compared between burnt and reference sites, significant differences were found for twelve of the 103 categories (Figure 4.3). Reference sites presented higher frequencies of taxa with reproduction via fixed eggs, aquatic active dispersal, resistance through diapause,

feeding on debris superior to 1mm, shredder feeding groups, respiration by gills and distribution along the metarhithron (fast flowing streams). Burnt sites, on the other hand, had higher frequencies of taxa with no resistance forms, with affinity to lower pH, eutrophic and polysaprobic waters and open water swimmers taxa. Mann-Whitney test results for the significant differences for individual trait frequencies between burnt and reference sites, on the sum of the four sampling periods (representing a year-round combined sample) and per sampling season are presented in Table 4.4.

Table 4.4 – Mann-Whitney test results for the significant differences on individual trait modality frequencies between burnt (Fire) and reference (Ref) sites based on pooled samples (four sampling occasions) and for respective sampling period.

Sampling period	Trait (modality)	Mann-Whitney U	p-value	Trend
All sampling periods	Reproduction (fixed eggs)	386.0	0.030	Ref > Fire
	Dispersal (aquatic active)	344.0	0.007	Ref > Fire
	Resistance form (diapause)	362.0	0.014	Ref > Fire
	Resistance form (none)	334.0	0.005	Fire > Ref
	Food (debris > 1 mm)	384.0	0.029	Ref > Fire
	Feeding group (shredder)	375.0	0.022	Ref > Fire
	Respiration (gills)	402.0	0.049	Ref > Fire
	pH preferences (< 4)	395.0	0.041	Fire > Ref
	Trophic degree (eutrophic)	387.0	0.031	Fire > Ref
	Saprobic value (polysaprobic)	401.0	0.048	Fire > Ref
	Longitudinal distribution (metarhithron)	368.0	0.017	Ref > Fire
	Locomotion (open swimmer)	380.0	0.025	Fire > Ref
November	Food (debris < 1 mm)	11.0	0.042	Fire > Ref
	Locomotion (flight)	10.0	0.031	Ref > Fire
	Locomotion (burrowing)	9.0	0.022	Fire > Ref
March	Saprobic value (β-mesoprobic)	10.0	0.050	Ref > Fire
May	Size (40-80 mm)	10.0	0.050	Fire > Ref
	Reproduction (fixed eggs)	5.0	0.008	Ref > Fire
	Feeding group (shredder)	2.0	0.002	Ref > Fire
	Feeding group (predator)	10.0	0.050	Fire > Ref
	Current preferences (slow waters)	10.0	0.050	Ref > Fire
August	Resistance form (none)	17.0	0.009	Fire > Ref

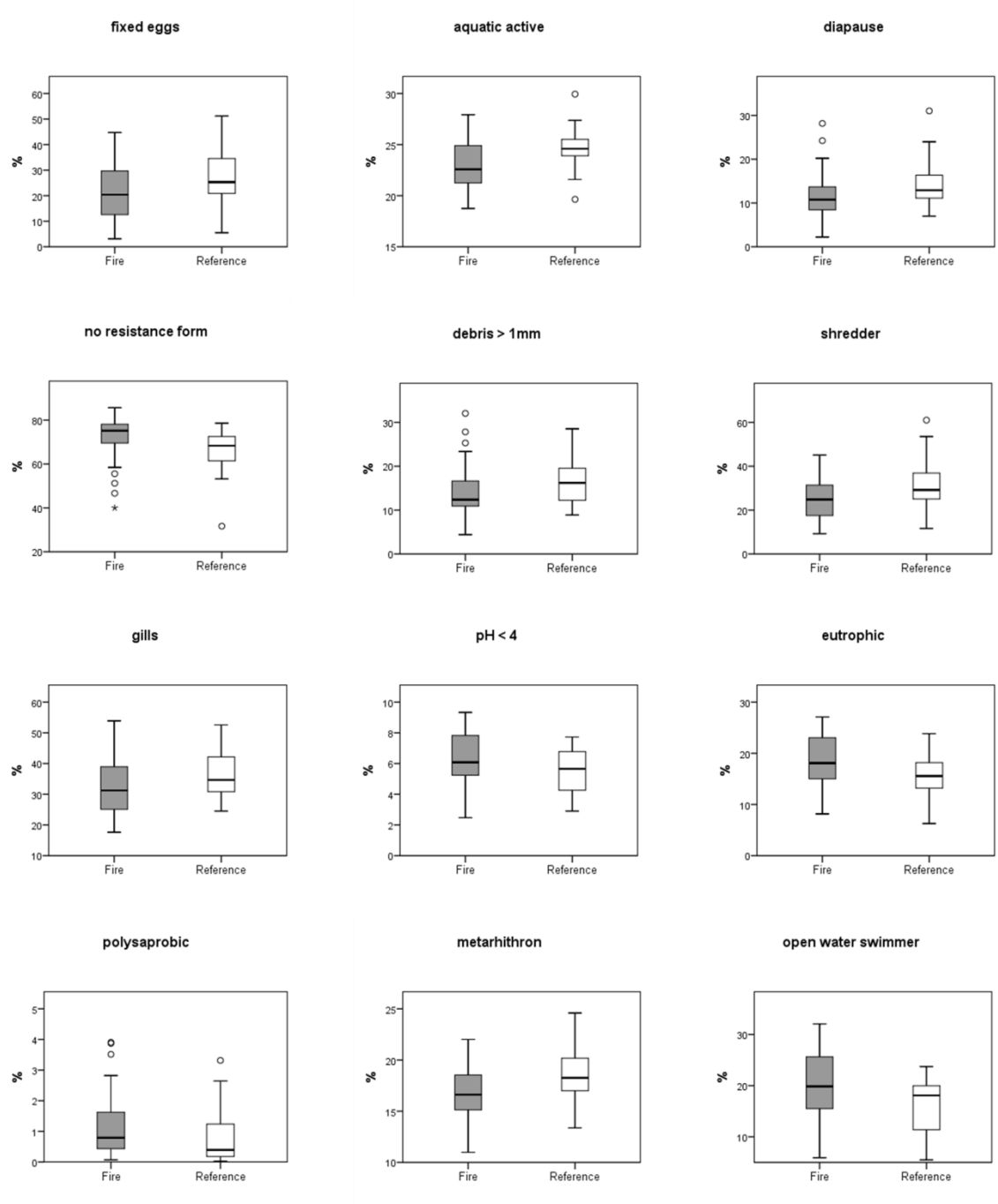

Figure 4.3 – Boxplots representing the variation of trait modality frequencies, for those categories where significant differences were found. Burnt sites are represented by the grey bars and reference sites are represented by the white bars.

4.3.3 Relationship between functional structure and environmental data

The RLQ analysis showed that the first axis accounted for 49.6% of the total co-inertia (i.e., the link between environmental variables and traits), while 22.6% was expressed on the second axis (Table 4.5). The global significance of the obtained model was p=0.033, meaning that there was a significant relationship between traits and environmental variables. The primary RQ axis present 38.7% correlation with taxa composition (table L), and explained 91.8% and 67.9% of the variance expressed by the environmental variables ordination (table R) and traits ordination (table Q), respectively (Table 4.5).

Table 4.5 - Results from RLQ analysis using environmental variables and taxa traits. a) Eigenvalues (and % of total co-inertia) for the first two axes for the separate ordinations: L (correspondence analysis – CA), tables R (principal components analysis - PCA) and Q (fuzzy correspondence analysis – FCA). b) Summary of RLQ analysis: eigenvalues and percentage of total co-inertia accounted for by the first two RLQ axes, covariance and correlation (and % variance) with L matrix, and projected variance (and % variance) with the R and Q matrices

		Axis 1(%)	***Axis 2 (%)***
a)	*Separate ordinations*		
	L Taxa (CA)	0.2050 (8.8%)	0.1634 (7.0%)
	R Environment (PCA)	4.7575 (29.7%)	3.2798 (20.5%)
	Q Traits (FCA)	0.1638 (11.9%)	0.1218 (8.9%)
b)	*RLQ analysis*		
	Eigenvalues	0.0149 (49.6%)	0.0069 (22.6%)
	Covariance	0.122	0.083
	Correlation L	0.175 (38.7%)	0.173 (60.4%)
	Projected variance R	4.367 (91.8%)	7.205 (98.6%)
	Projected variance Q	0.111 (67.9%)	0.198 (49.1%)

The first RLQ axis was positively associated with altitude, stream features and water quality and negatively associated with conductivity, temperature and percentage of forest. This trend, towards up-land streams, with faster currents,

lower conductivity, larger substrates, moss vegetation and land use dominated by scrublands were negatively associated with multivoltanism and positively associated with eggs in an aquatic stage and crawling. There was also a positive association with traits directly linked with microhabitat preference, such as larger substrate size instead of silt and clay and for rhithron instead of potamon (Figure 4.4).The second RLQ axis was associated with lower temperatures and altitude, smaller streams (with narrower channels and shallower water), higher slopes and forest cover percentage in the catchment but lower riparian complexity. This axis was also positively related to artificial embankments. Associated with these environmental features were biological traits including oviviparity, cold thermal preferences, intolerance to higher pH values and preference for lower saprobic values (Figure 4.4).

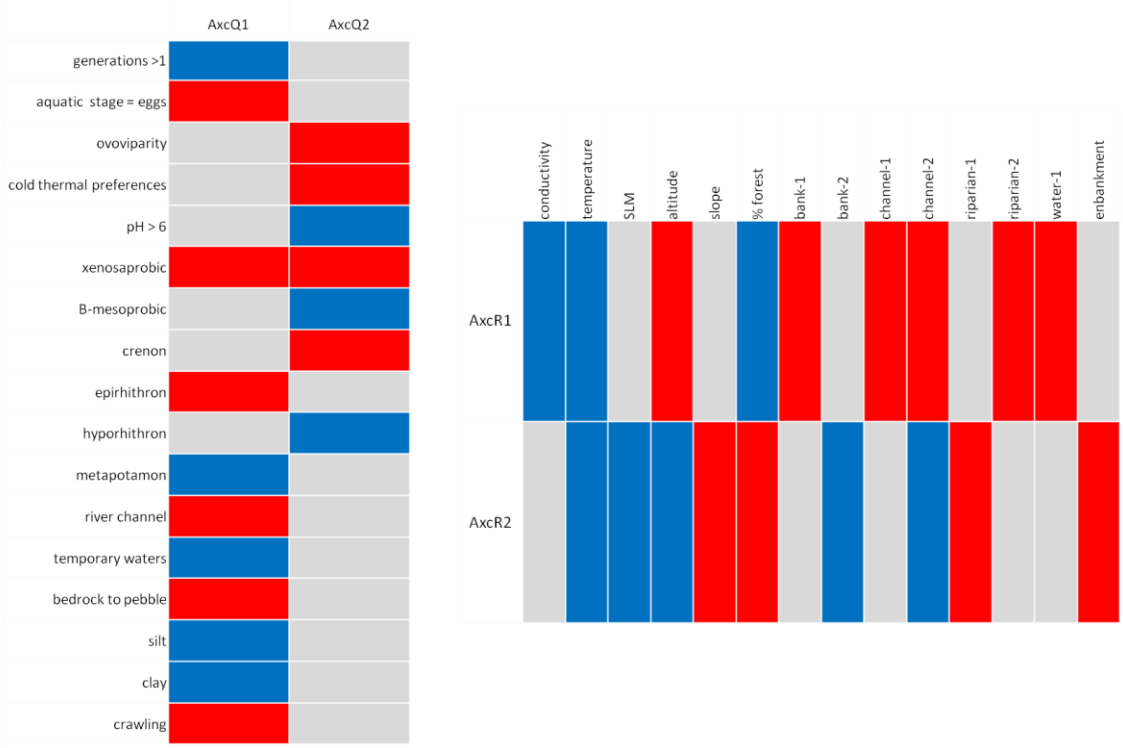

Figure 4.4 – Fourth corner analysis results (only significant correlations with at least one RLQ axis are presented). Blue squares represent negative associations, red squares represent positive associations and grey no significant correlation.

4.4 Discussion

4.4.1 Impact of fire on Functional Diversity (FD)

Overall, functional diversity indicated no clear difference between burnt sites and references sites. Only at the time of one year after the fire, some differences were found, with reference sites showing higher diversity on some traits connected to reproduction and dispersal. Fire disturbance is strongly related to increased erosion and sediment loading (Arkle *et al*., 2010); previous research has indicated that macroinvertebrate trait diversity can show a weak response to hydromorphological alteration (Feld *et al.,* 2014)

Bêche and Statzner (2009), in a large scale study concerning taxonomy versus trait-based approach to determine macroinvertebrate richness gradients in European and American streams, stated that, in Europe, the saturation in terms of functional richness is achieved with 30 genera. For the present work, 177 genera were identified, and the richness per site ranged from 19 to 91 taxa. The lowest taxa richness values (inferior to 30 taxa) was observed on few sites (12%), and only for the March sampling period. Is it possible that, given the high natural diversity present in up-land Portuguese streams (Graça *et al.,* 2004), what Bêche and Statzner called “functional redundancy” is easily achieved. In order to circumvent the limitations of a taxonomic richness approach, a diversity index was used that takes into account abundance, since the importance for a given ecosystem function would be different if performed by one or by a large number of individuals. Nevertheless, previous studies have shown a high correlation between functional richness and functional diversity (Bêche and Resh, 2007; Mouchet *et al.*, 2010), which could explain the limited usefulness of the chosen metric to elucidate the impact of fire in our study.

4.4.2 Impact of fire on functional structure

With rainfall after a fire event, erosion and floods can transport large volumes of ash and burnt wood into the streams causing channel modifications

and decreasing channel stability (Benda *et al*., 2003; Vaz *et al*., 2011; Vaz *et al*., 2013). This fact may explain the lower percentage of traits categories linked with substrate stability at burnt sites, such as the lower proportion of reproduction by fixed eggs and the higher percentage of open water swimmers. Likewise, in a work describing the effects of fire on macroinvertebrate communities in NE Spain Verkaik *et al*., (2014) reported that three out of 22 analyzed traits demonstrated a response to fire impacts. Vervaik et al (2014) also found differences on traits related to reproduction and taxa attachment to the substrate. In their study, multivoltine taxa, endobenthic and temporarily attached animals, were also selected as important features and were found in lower proportion on burnt sites.

Traits relating to water quality were indicative of higher tolerance at burnt sites, with a predominance of categories such as eutrophic, polysaprobic, and lower pH preferences. This may be due to the deterioration of water quality that can follow fire impact (Rinne, 1996; Hall and Lombardozzi, 2008). Respiration by gills, less frequent in burnt sites, might also be related to an increase of fire-related suspended material.

In our study, we found differences in the type of food consumed and feeding mechanisms, describing a trend from more specialized types of feeding (like shredders) in reference sites, towards more flexible feeding strategies (like predators) in burnt sites. These alterations in food webs have been previously described in fire-related studies such as in Mihuc and Minshall (2005) and Vieira *et al*. (2004). Some studies also reported the inability of macroinvertebrates to feed on burnt material, which might also explain the lower percentage of shredders observed in this study (Mihuc and Minshal, 1995; Gama *et al.,* 2007).

4.4.3 Relationship between functional structure and environmental data

Although the RLQ and fourth corner analysis showed a relationship between environmental characteristics and traits, no association was found between the specific variables concerning fire and traits.

The primary axis of RLQ analysis shows the natural trend of Portuguese streams, where conductivity and temperature decrease inversely with altitude. It also reveals the tendency of upland low-order streams to have less riparian complexity, less shade, faster flow, larger substrate size, less cover and in-stream vegetation dominated by moss. This natural tendency is associated with a set of traits including distribution along the river, mesohabitat (Hildrew and Giller, 1994) and microhabitat that clearly described the ecological preferences and requirements of up-land streams macroinvertebrate communities. This data suggests that this type of approach has ecological relevance despite failing to identify a clear trait-based response to wildfire.

4.4.4 Final remarks

The use of biological traits has proved useful to determine sensitivity of macroinvertebrate communities to toxicity (Baird and Van Den Brink, 2007), hydrological disturbances and flow alterations (Bonada *et al.,* 2007b; Brooks *et al*., 2011, Walters, 2011) and climate change (Poff 2010; Conti *et al.*, 2014; Sandin, 2014). A trait-based approach, despite potentially offering useful insight about the processes associated with fire impact and recovery, did not demonstrate a clear response according to the comparative analysis conducted in this study. This suggests that, in the case of fire disturbance, traits-based analysis should be applied with caution and in combination with other traditional approaches and metrics, such as taxa richness, abundance or community structure, measures that demonstrated a clear response of macroinvertebrates in previous works (see chapter 2 and 3).

4.5 References

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5 Concluding Remarks

Macroinvertebrate communities play an important role in stream ecosystems. As consumers representing various trophic levels, they influence nutrient cycling, primary production and decomposition, in addition to serving as food source for higher trophic levels (Wallace and Webster, 1996). Therefore, disturbances affecting macroinvertebrates affect the ecological functions of lotic ecosystems.

In many Ecology studies, time scale represents a major practical constraint. Given the great discrepancy between the existing data on fire impact and recovery time of macroinvertebrate communities, from very different eco-regions and contexts, ranging from only one year (e.g. Minshall *et al.*, 1997; Earl and Blinn, 2003) to 4 years or more (e.g. Richards and Minshall, 1992; Vieira *et al.*, 2004), the analytical approach was to first describe long/mid-term effects and subsequently the short-term effects, to determine the time window in which fire disturbance operates in the specific case of Portuguese up-land streams.

Chronosequence, a technique in which space substitutes time, allowed interpretation over a longer time scale. All the parameters measured on our long-term study (abundance, taxa richness and community structure) showed signs of recovery on these parameters after two years. This highlighted the need to better understand the short-term (0-1 year) recovery process, and lead to a focus on the mechanisms taking place on the first year after fire impact, and comparing it with natural seasonal changes on unburnt reference areas.

The short-term survey results showed that both taxa richness and abundance parameters declined markedly after rain events. This is consistent with the theory that the effects associated with post-fire flood, such as increased erosion, wood and sediment transportation and channel modification, were the major cause of the depletion on macroinvertebrate communities (Roby and Azuma, 1995; Rinne, 1996; Minshall, 2003; Viera *et al.*, 2004, Mellon *et al.*, 2008).

In order to obtain a more holistic perspective of fire impact, after studying community end-points, we focused on some measures of ecological function, applying a trait-based approach on short-term data. At the functional level, we

found almost no differences on functional diversity during the first year after of fire occurrence, between burnt and reference sites. Only a few specific differences on functional structure were found, such as food and feeding habits, reproduction, resistance forms and ecological preferences. Despite the effect on taxa richness, and even a more marked affect on species abundance, community function was not altered in the same degree.

Summarizing all these evidences, we hypothesize that fire impact acts as a generalized pulse disturbance, removing individuals indiscriminately, more than selecting a certain set of traits. This, together with the high initial species richness on the studied streams, would justify the decrease on individual abundance (also leading to the disappearance of rare species) without a concomitant change in the general functional diversity or structure during the first year after fire impact.

For all of this, we suggest that Portuguese macroinvertebrate communities do not show a high resistance to fire disturbance. Nevertheless, resilience seems to be a feature of these communities. Naturally shaped by evolutionary pressures such as floods, droughts and fire events, these communities present a remarkable capacity for recovery from disturbance to a pre-fire state. Recently burnt sites supported a high abundance of good colonizers, such as mayflies, with short generation times and high reproduction rates. Our data also suggests a rapid adaptation of food webs, with taxa from more specialized feeding groups (like shredders), being replaced by more generalist feeders (like predators).

Given the marked effects found on abundance, richness and community structure level and the inconclusive results of functional approach, we advice that post-fire monitoring of macroinvertebrate communities should focus on taxonomic and density metrics, using functional measures as complement. In the specific case of the response of macroinvertebrate communities to fire disturbance, at least in Portugal, a trait-based approach only cannot substitute the traditional taxonomic approach.

Throughout this study, we attempted to connect the variation on biological communities and its environmental context, aiming to determine the characteristics that make a stream more susceptible to fire disturbance.

Our results supported the importance of stream size (small rivers seem, indeed, to be more vulnerable) and of extension of catchment affected, as suggested by other authors (Rinne, 1996; Minshal *et al.,* 1997). Both long-term and short-term surveys revealed the importance of complex riparian vegetation to mitigate the effects of fire impact and promote quick re-colonization, as stated by other authors (Dwire and Kauffman, 2003; Petit and Naiman, 2007).

Other variables that seem to influence the recovery of macroinvertebrate communities in the case of fire impact are channel modifications, caused by large amounts of sediment input and wood debris that reach streams during post-fire floods (Benda et al., 2003; Dunham et al., 2007; Bendix and Cowell, 2010). These hydrogeomorphologic alterations are deeply connected with stream substrate size and stability, whose importance for macroinvertebrates was confirmed by the differences recorded between burnt and reference sites on substrate-dependent traits, such as microhabitat preferences, types of locomotion and reproduction strategies that involve substrate fixed stages.

Furthermore, we confirm that artificial embankment of stream channels, a widespread practice in Portugal that negatively interfere with natural flow and sediment transportation (Cortes *et al*., 2002; Monaghan and Soares, 2008), can also delay the post-fire recovery, constituting additional challenge on river restoration post-fire disturbance.

The knowledge of this environmental features that influence fire disturbance and recovery would be crucial information for post-fire management and restoration, for instance, in the prioritization of the application of strategies for erosion mitigation.

As future work on this field, mid-term studies with frequent surveys could be helpful to better understand the steps of post-fire succession and the recolonization processes involved (drift, aerial dispersal, up-streams

movements). Focus should be given to the most susceptible streams that take longer to recover.

Moreover, since a decrease of abundance was noticed in the present work, the study of the impacts of macroinvertebrate post-fire depletion on higher trophic levels, such as fish and amphibians populations, would be very valuable and would contribute to a more global perspective on fire disturbance.

5.1 References

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